UNIVERSITÉ DU QUÉBEC À TROIS-RIVIÈRES

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UNIVERSITÉ DU QUÉBEC À MONTRÉAL

IMPACTS D'UNE AUTOROUTE SUR LES POPULATIONS D'OMBLE DE FONTAINE EN RIVIÈRE

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PAR
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L'humanité est à un croisement
Un chemin mène au désespoir
L'autre à l'extinction totale
Espérons que nous aurons la sagesse de savoir choisir

Woody Allen

Dualité

Les rivières sont des chemins qui marchent,
Et qui portent où l'on veut aller

Blaise Pascal

AVANT-PROPOS

Les chapitres I, II, et III de cette thèse sont présentés sous forme d'article scientifique. Les données analysées dans ces trois chapitres proviennent des travaux de terrain pour lesquels j'ai activement participé. J'ai contribué à l'élaboration du plan d'échantillonnage en collaborations avec mes co-directeurs. La logistique ainsi que l'encadrement des assistants de recherche ont relevé de la responsabilité d'Yves Paradis et moi-même. Je confirme avoir rédigé toutes les premières versions des articles présentés et intégré les révisions et suggestions faîtes par mes co-directeurs suite à leurs lectures des manuscrits. Ces trois articles scientifiques ont été ou seront soumis à des revues scientifiques avec comités de lecture. Le premier chapitre a été soumis au périodique *Journal of Applied Ecology* et est actuellement en révisons. Le deuxième chapitre sera soumis au périodique *Ecological Applications*. Le troisième chapitre sera soumis au périodique *Journal of North American Benthological Society*. Ce dernier chapitre a été écrit en collaboration avec Jan Franssen en plus de mes co-directeurs.

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RÉSUMÉ

Les impacts de la fragmentation de l'habitat sur la distribution et l'abondance des populations sont actuellement des enjeux majeurs en écologie. La réduction de la connectivité causée par la fragmentation de l'habitat modifie la dynamique des populations et menace de nombreuses espèces animales. En particulier, les infrastructures routières fragmentent durablement le paysage. La sédimentation induite par les travaux autoroutiers et la restriction des déplacements au niveau des traverses sont les deux principaux impacts des routes sur les populations de poissons.

L'objectif de la thèse a été d'évaluer les modifications de la distribution spatiale des populations d'omble de fontaine (*Salvelinus fontinalis*) à proximité d'un axe routier, en proposant des mécanismes conduisant au patron observé. Les deux mécanismes abordés ont été la dispersion estivale des individus et la sélection des sites de reproduction à l'automne. Cette thèse s'est intégrée au projet d'élargissement de l'axe routier 73/175 entre les villes de Québec et de Saguenay, entrepris par le ministère des Transports du Québec et dont la réalisation est prévue de 2006 à 2012. Dans cette région, l'omble de fontaine est l'espèce dominante pouvant être affectée par la réfection de l'autoroute.

Un plan d'échantillonnage extensif incluant 38 cours d'eau sur un parcours linéaire de 157 km a été retenu pour suivre les travaux autoroutiers de 2006 à 2008. La densité d'omble de fontaine a été estimée par pêche électrique sur 36 cours d'eau pendant trois étés consécutifs et les impacts autoroutiers, évalués grâce à l'utilisation des modèles mixtes. L'approche par modèles mixtes est une alternative flexible et puissante aux approches analytiques traditionnelles dans les études de type BACI (Before After Control Impact) pour modéliser et pour quantifier les impacts d'origine humaine tout en tenant compte de la structure hiérarchique des données. Par ailleurs, un cadre de modélisation général a été développé pour quantifier à la fois la dispersion estivale des individus et la perméabilité des traverses à partir de données de marquage – recapture. Ces données proviennent de quatre cours d'eau dont les traverses étaient représentatives de celles qui seront en place suite à la réfection de l'autoroute et dont le niveau de franchissement était considéré élevé. Enfin, les sites de reproduction de l'omble de fontaine aux automnes 2007 et 2008 ont été cartographiés sur 11 cours d'eau avec une résolution spatiale très fine en vue de l'estimation des impacts des travaux autoroutiers sur la reproduction.

Nos résultats indiquent que la fragmentation de l'habitat engendrée par des traverses dont le niveau de franchissement n'est pas approprié est le processus principal qui structure la distribution spatiale des populations d'omble de fontaine à

proximité de l'axe routier. Les traverses sans substrat naturel, dépourvues d'aménagement pour faciliter le passage du poisson ou présentant un seuil ont affiché des densités moyennes (estimées sur les 800 premiers mètres de part et d'autre de l'axe routier) qui étaient deux à six fois supérieures en aval par rapport à l'amont. Le mécanisme le plus plausible pour expliquer ces différences de densité est une restriction des déplacements vers l'amont. La faible dispersion estivale (< 10 m pour 48 à 72 % de la population) suggère que l'effet de barrière ne joue pas un rôle majeur sur la dynamique des populations à cette période de l'année. La restriction des déplacements pourrait se faire ressentir à d'autres périodes critiques dans le cycle vital, comme plus tôt au printemps ou pendant la migration à l'automne. De plus, l'estimation de la perméabilité des nouvelles traverses suggère une libre circulation du poisson, ce qui est cohérent avec la distribution spatiale observée pour ce type de traverse.

La construction autoroutière n'a pas eu d'impact à court terme sur la densité de populations locales d'omble de fontaine, ce qui pourrait s'expliquer par des mesures de rétention des sédiments efficaces lors des travaux autoroutiers. Par ailleurs, une diminution du nombre de sites de reproduction, légère mais significative, a été observée à l'automne 2008. La combinaison des travaux autoroutiers et des conditions météorologiques extrêmes auraient pu être à l'origine de cette diminution. Toutefois, le nombre de sites de reproduction semble être davantage gouverné par des variables du paysage que par les travaux autoroutiers.

En conclusion, la distribution spatiale des populations d'omble de fontaine à proximité de l'axe routier est essentiellement influencée par le type de traverses et non par les activités de construction. Le mécanisme le plus plausible pour expliquer cette distribution est la restriction des déplacements survenant à une autre période que l'été. Les approches de modélisation développées dans cette thèse proposent des mesures quantitatives de la fragmentation de l'habitat qui peuvent facilement être implémentées dans les programmes de suivi pour une évaluation rigoureuse des impacts autoroutiers sur les populations de poisson en rivière.

Mots-clés : barrière, densité, dispersion, écologie des routes, évaluation des impacts environnementaux, fragmentation, marquage, modèles mixtes, modélisation, reproduction, sédimentation, simulation

INTRODUCTION GÉNÉRALE

Impacts des routes sur les écosystèmes : du terrestre à l'aquatique

Les routes ont un impact grandissant sur les écosystèmes (Forman et Alexander 1998, Trombulak et Frissell 2000, Fahrig et Rytwinski 2009, Laurence et al. 2009, Benítez-López et al. 2010). Chemins forestiers, routes, autoroutes, etc., nombreuses sont les infrastructures de transport qui façonnent notre paysage. Riitters et Whickham (2003) estimaient par exemple qu'aux États-Unis, 20 % des terres étaient à moins de 127 m d'une route et que seulement 3 % des terres étaient éloignées de plus de 5 176 m de la route la plus proche. Devant ces faits sans équivoque, il apparaît essentiel de comprendre comment les espèces animales et végétales réagissent face à cette modification de leur habitat (Forman et Alexander 1998, Jaeger et Fahrig 2004). Un premier ouvrage résume les impacts des routes sur les écosystèmes et met en évidence les principaux enjeux environnementaux sous un terme unificateur « road ecology », que nous traduirons en français par « l'écologie des routes » (Forman et al. 2003). De manière générale, l'écologie des routes est l'étude des interactions entre les organismes vivants et le réseau routier (Forman et al. 2003). Cette nouvelle discipline est une science appliquée et combine plusieurs champs théoriques de recherche dont, principalement, la fragmentation de l'habitat (Fahrig 2003) et la biologie de la conservation (Fahrig et Merriam 1994, Benítez-López et al. 2010). Les paragraphes suivants exposent le cadre conceptuel de la fragmentation de l'habitat appliqué à l'écologie des routes, en démontrant comment les connaissances acquises en milieu terrestre peuvent être transposables au milieu aquatique. Enfin, le dernier paragraphe souligne les principaux objectifs actuels de conservation lors de la planification des infrastructures routières.

La fragmentation de l'habitat, au sens large du terme, se compose de deux processus distincts : la fragmentation *en soit*, qui représente la division d'un habitat anciennement continu, et la perte d'habitat, qui représente la réduction de la quantité d'habitats disponibles sur le territoire (Fahrig 2003). Le réseau routier est un cadre idéal pour l'étude de ces deux processus puisqu'il entraîne à la fois un morcellement du territoire et une perte d'habitat. Il est à noter que la perte d'habitat excède souvent la superficie du réseau routier en raison du comportement d'évitement des organismes (« road-effect zone », *sensu* Forman et Alexander 1998). Par exemple, lors d'une méta-analyse portant sur 49 études et regroupant 234 espèces d'oiseaux et de mammifères, Benítez-López *et al.* (2010) ont trouvé une diminution de l'abondance des espèces à proximité des routes qui se faisait ressentir sur environ un kilomètre pour les oiseaux et cinq kilomètres pour les mammifères.

En milieu terrestre, la mortalité par collision a été un des premiers impacts étudiés des routes sur la faune (Stoner 1925, Hels et Buchwald 2001, Clevenger et al. 2003). Toutes les espèces n'ont cependant pas le même facteur de risque de collision. Les amphibiens, les reptiles et la plupart des animaux à mobilité réduite sont généralement plus susceptibles de mourir par collision lorsqu'ils tentent de traverser une route (Stoner 1925, Fahrig et Rytwinski 2009, Laurence et al. 2009). Afin de réduire la mortalité par collision et par règle de sécurité routière (surtout dans les cas de collision avec la grande faune), des clôtures peuvent être installées le long des axes routiers. Ces mesures de mitigation ont conduit à la production d'une littérature abondante, portant sur les déplacements des organismes à proximité des routes et sur les conséquences de l'effet de barrière sur la dispersion et la viabilité des populations (Jaeger et Fahrig 2004, Jaeger et al. 2005, McGregor et al. 2008, Shepard et al. 2008). L'effet de barrière des routes sur la dispersion des organismes entraîne rapidement une fragmentation des populations et une baisse de la diversité génétique (Epps et al. 2005, Clark et al. 2010). L'outil moléculaire constitue en ce sens une technologie de pointe pour étudier ces types d'impacts (Balkenhol et Waits 2009).

En milieu aquatique, des impacts similaires sont attendus comme l'altération physique et chimique de l'environnement, la fragmentation de l'habitat et l'augmentation de la mortalité (Trombulak et Frissell 2000, Wheeler et al. 2005). Toutefois, en opposition à la mortalité par collision en milieu terrestre, la mortalité engendrée par la sédimentation ou les polluants tend à être asymétrique en milieu aquatique, puisque les effets se font ressentir majoritairement en aval des routes (Forman et Alexander 1998, Wheeler et al. 2005, Meland et al. 2010). En effet, le réseau hydrologique est particulièrement altéré aux intersections avec les routes, ce qui entraîne en aval de ces dernières des débits de pointe plus élevés, une sédimentation accrue et des risques d'embâcle au niveau des structures (Jones et al. 2000, Benda et al. 2004). De manière générale, la sédimentation (perte d'habitat) et l'obstruction à la libre circulation des poissons (fragmentation *en soit*) sont les deux principaux impacts environnementaux pouvant conduire à des modifications de la distribution et de l'abondance des poissons à proximité des routes (Wheeler et al. 2005). Ainsi, il apparaît que le cadre conceptuel de l'écologie des routes plus largement développé pour le milieu terrestre et brièvement exposé plus haut s'applique également au milieu aquatique.

La sédimentation est un impact d'origine généralement humaine qui menace la plupart des écosystèmes aquatiques (Waters, 1995, Sutherland et al. 2002, Scheurer et al. 2009). Ces impacts se font particulièrement ressentir lors des phases de constructions routières (Forman et Alexander 1998, Wheeler et al. 2005). Les espèces nécessitant un substrat propre et dépourvu de sédiments fins sont reconnues pour être les plus affectées par la sédimentation (Sutherland et al. 2002, Scheurer et al. 2009). Plus spécifiquement, les plus fortes mortalités sont observées pour les stades allant de l'œuf à l'émergence des larves (Jensen et al. 2009, Guillemette et al. 2011). En réduisant l'abondance et la disponibilité des invertébrés benthiques (Culp et al. 1986, Hedrick et al. 2010), le transport et le dépôt de sédiments fins peuvent aussi réduire la croissance et la survie des poissons dans un court intervalle de temps (Shaw et

Richardson 2001, Suttle et al. 2004). De même, la turbidité peut diminuer l'efficacité de capture des proies (Sweka et Hartman 2001) ou le retour des adultes sur les sites de reproduction (Whitman et al. 1982). L'effet combiné de ces différents facteurs pourrait conduire à une diminution de l'abondance des poissons en lien avec l'augmentation de la sédimentation (Nakamura et al. 1994, Scheurer et al. 2009).

La connectivité hydrologique est actuellement un enjeu majeur (Fullerton et al. 2010). Dans ce contexte, l'intégration de l'effet de barrière au sein des réseaux hydrographiques est essentielle à la compréhension de la dynamique des populations de poissons en rivière (Letcher et al. 2007, Schick et Lindley 2007). Les structures physiques mis en place sur les cours d'eau lors de la construction des voies de transport (ex. ponceau) peuvent être une entrave à la libre circulation des poissons (Belford et Gould 1989, Warren et Pardew 1998, Burford et al. 2009, Norman et al. 2009, Bouska et Paukert 2010). Dans ces articles, la pente et la longueur de l'ouvrage, la vitesse d'écoulement sous l'ouvrage et la présence d'un seuil font partis des principaux facteurs impliqués dans la restriction des déplacements. La détermination de critères de passage des espèces et des stades de vie visés (Bjorn et Reiser 1991, Love et Taylor 2003) oriente le travail des ingénieurs lors de la conception des ouvrages, afin d'assurer la libre circulation des poissons sous les ouvrages (Ead et al. 2002, Larinier 2002). D'autre part, ces mêmes critères peuvent être utilisés dans une optique de gestion globale pour classifier les ouvrages suivant le niveau de franchissement et pour donner priorité à la restauration des ouvrages les plus dommageables au maintien des populations au sein du bassin versant (Steel et al. 2004, Gibson et al. 2005, Meixler et al. 2009, Poplar-Jeffers et al. 2009).

Les enjeux de conservation en lien avec le développement des infrastructures routières s'orientent de plus en plus vers de grandes échelles spatiales (Weber et Allen 2010, van der Ree et al. 2011). La planification du réseau routier gagne à être conduite en collaboration avec les scientifiques afin d'obtenir des tracés minimisant

les impacts sur les écosystèmes et assurant le maintien de la connectivité entre les habitats essentiels à la préservation des populations (Gurrutxaga et al. 2010, Quintana et al. 2010). Par exemple, Colchero *et al.* (2011) ont conduit une étude de télémétrie afin de déterminer les passages les plus fréquentés par le Jaguar (*Panthera onca*), ce qui permettra d'optimiser la localisation des traverses lors de la planification du tracé routier. En contrepartie, les scientifiques doivent tirer profit de l'expertise des ingénieurs dans l'efficacité des mesures de mitigation à mettre en place (Shields 2009, Collins et al. 2010). Dans tous les cas, les recherches doivent mieux évaluer les impacts des routes à de grandes échelles spatiales et ont avantage à passer par l'élaboration d'un plan d'échantillonnage approprié et une analyse rigoureuse permettant de porter des conclusions fiables ayant un fort pouvoir d'inférence (Roedenbeck et al. 2007, Robinson et al. 2010).

Évaluation des perturbations environnementales

L'évaluation des perturbations environnementales a largement été débattue dans la littérature scientifique au cours des 30 dernières années (Stewart-Oaten et al. 1986, Eberhardt et Thomas 1991, Green 1993, Underwood 1994, Stewart-Oaten et Bence 2001, Underwood et Chapman 2003, Bennett et Adams 2004). En particulier, Downes *et al.* (2002) ont publié un ouvrage spécialement dédié au suivi des impacts écologiques en milieu fluvial. De ce fait, l'objectif de cette section n'est pas de faire une revue détaillée des forces et des faiblesses des divers plans d'échantillonnage et des analyses statistiques utilisés, mais plutôt de dresser un portrait global de l'évaluation des perturbations environnementales, en faisant ressortir les principaux facteurs à considérer et les défis à relever.

Une des difficultés majeures des évaluations environnementales est de réussir à isoler la perturbation d'origine humaine de la variabilité naturelle (Walters et al. 1988, Osenberg et al. 1994, Underwood 1994). En effet, toute la question est de

savoir si les changements observés dans la variable réponse (ex. abondance, diversité, etc.) suite à une perturbation d'origine humaine (ex. barrage, route, rejet industriel, etc.) diffèrent des changements qui se seraient produits en l'absence de perturbation. Le couplage d'un site témoin (c'est-à-dire non affecté par la perturbation) avec le site altéré (c'est-à-dire affecté par la perturbation) et le suivi de ces sites avant et après la perturbation a pour but de détecter les impacts tout en tenant compte de la variabilité naturelle et constitue le plan d'échantillonnage standard de l'approche de type BACI (« Before–After Control–Impact » ; Stewart-Oaten et al. 1986, Green 1993, Smith et al. 1993). Le site témoin peut agir au même titre qu'une covariable et devrait idéalement être comparable au site altéré (Stewart-Oaten et al. 1986, Downes et al. 2002). L'utilisation de plusieurs sites témoins (« beyond BACI » ; Underwood 1992, Underwood 1994, Benedetti-Cecchi 2001), voire de plusieurs sites altérés (MBACI ; Keough et Quinn 2000, Downes et al. 2002, Angeler et Moreno 2007), améliore la quantification de la variabilité naturelle, augmente le pouvoir d'inférence et diminue la probabilité selon laquelle les différences observées entre les sites témoins et altérés soient le fruit du hasard. Toutefois, lorsque la perturbation survient en même temps qu'une modification environnementale, il devient difficile de déterminer quelle est la cause des changements éventuellement observés. Un plan d'échantillonnage en palier consiste à échelonner dans le temps le début de la perturbation, ce qui permet de contrôler adéquatement les interactions « temps–perturbations » (Walters et al. 1988). Ce plan d'échantillonnage n'est cependant pas possible dans le cas des accidents environnementaux (Stewart-Oaten et al. 1992, Wiens et Parker 1995).

De manière générale, la comparaison des trajectoires entre les sites témoins et altérés est l'approche de base utilisé dans la détection des impacts (Stewart-Oaten et al. 1986, Underwood 1992). Ces impacts peuvent se manifester par une diminution (ou augmentation) ponctuelle (ou continue) de la moyenne (ou de la variabilité) de la variable réponse (Underwood 1994, Downes et al. 2002). Devant la multitude des réponses possibles, la réflexion sur les effets attendus de la perturbation et le temps de

récupération du système est une étape essentielle conduisant à l'énoncé d'hypothèses claires (Parker et Wiens 2005, Hewitt et al. 2007). A l'intérieur de ces hypothèses, le terme d'interaction, généralement entre la période d'échantillonnage (avant – après perturbation) et le traitement (site témoin – site altéré), est au cœur des études d'évaluation d'impacts (Green 1993, Smith et al. 1993, Underwood 1994). Ce terme d'interaction indique si la variable réponse diffère entre les sites témoins et altérés suite à la perturbation et est considéré comme un instrument de mesure dans la détection des perturbations environnementales (Green 1993).

Les impacts environnementaux surviennent souvent à différentes échelles spatiales et temporelles, ce qui crée un défi tant sur le plan de l'échantillonnage que sur le plan des analyses statistiques (Hewitt et al. 2001, Stewart-Oaten et Bence 2001). Les deux principales questions soulevées sont : (1) est-ce que les sites témoins sont hors de la zone d'influence de la perturbation et (2) comment tenir compte de l'autocorrélation à la fois spatiale et temporelle des données récoltées ? Pour cette dernière question, il existe à présent des techniques d'analyse telles que les modèles mixtes et les modèles mixtes généralisés permettant de modéliser adéquatement les variabilités spatiales et temporelles inhérentes à la structure hiérarchique des plans d'échantillonnage (McDonald et al. 2000, Wagner et al. 2006, Deschênes et Rodríguez 2007). Ces techniques d'analyse s'avèrent particulièrement pertinentes pour des impacts se produisant à de grandes échelles spatiales. À de telles échelles, un niveau de réplication insuffisant est souvent vu comme une limite des plans d'échantillonnage et ne permet pas de discriminer efficacement la variabilité à l'intérieur et entre les sites témoins et altérés (Murtaugh 2000, Lierman et Roni 2008). Les routes sont un exemple de perturbations qui gagnent à être étudiées à de grandes échelles spatiales, de par l'étendue des réseaux routiers et des habitats critiques à préserver pour la persistance des populations (Riitters et Wickham. 2003, Roedenbeck et al. 2007, van der Ree et al. 2011). Dans leur agenda de l'écologie des routes, Roedenbeck *et al.* (2007) recommandent les approches de type BACI (telles

qu'exposées plus haut) pour une meilleure évaluation des impacts des routes sur la dynamique des populations.

Contexte et objectifs de la thèse

Le cadre conceptuel de l'écologie des routes, adapté à l'écologie aquatique, l'intégration des principes fondamentaux dans les évaluations des perturbations environnementales et l'utilisation des analyses statistiques de pointe sont intégrés dans les objectifs de cette thèse afin de comprendre les impacts des travaux autoroutiers sur les populations d'omble de fontaine (*Salvelinus fontinalis*). Cette thèse s'intègre dans le projet d'élargissement de l'axe routier 73/175 de deux à quatre voies divisées et à chaussées séparées. Il s'agit d'un projet de construction majeur conduit par le ministère des Transport du Québec et dont la réalisation est prévue de 2006 à 2012. L'axe routier traverse la réserve faunique des Laurentides et le parc national de la Jacques-Cartier sur 174 km entre les villes de Québec et du Saguenay (Québec, Canada).

Dans cette région, l'autoroute est la seule perturbation anthropique sur le milieu aquatique. La zone d'étude se trouve sur le plateau laurentien à une altitude comprise entre 190 et 820 m et sous un climat continental humide, particulièrement rigoureux (température annuelle : 0.3 °C ; chute de neige annuelle : 639 cm). La végétation est composée d'une forêt boréale continue appartenant au sous-domaine de la sapinière à bouleau blanc de l'Est, dominée par le sapin baumier. La géologie est très homogène et se compose d'un socle rocheux métamorphique (massif gneissique) avec des roches intrusives (principalement des mangérites). Les cours d'eau sont majoritairement formés par des dépôts glaciaires et fluvio-glaciaires. Les cours d'eau de tête représentent une large proportion du réseau hydrographique. Ils sont sensibles aux perturbations environnementales et souvent sous représentés dans les recherches (Lowe et Likens 2005). Nous avons concentré nos efforts sur les petits cours d'eau de

tête en échantillonnant, de 2006 à 2008, un total de 37 cours d'eau répartis sur un parcours linéaire de 157 km. Les impacts de l'axe routier ont été évalués essentiellement sur le premier kilomètre de part et d'autre de l'emprise.

L'omble de fontaine est originaire de l'est de l'Amérique du Nord, mais en raison de son introduction par l'homme et de sa plasticité, on le retrouve actuellement un peu partout sur le continent (Power 1980). Au cours de sa vie, l'omble de fontaine est contraint de se déplacer entre des zones de reproduction, d'alimentation et de refuge pour satisfaire l'ensemble de ses besoins vitaux (Curry et al. 1997, Curry et al. 2002, Petty et al. 2005). Par exemple, les zones de reproduction et de croissance sont généralement dans les parties amont des cours d'eau (Curry et al. 2002, Petty et al. 2005), alors que les adultes regagnent l'aval du cours d'eau principal pour passer l'hiver (Curry et al. 2002). Enfin, les variations spatiales et temporelles de la fraie et des déplacements interagissent pour déterminer la distribution de l'omble de fontaine à l'échelle du bassin versant (Petty et al. 2005). L'omble de fontaine peut être affecté à la fois par la sédimentation (Guillemette et al. 2011) et par la fragmentation de l'habitat (Letcher et al. 2007), ce qui en fait un bon modèle pour l'étude des impacts des routes sur la dynamique des populations de salmonidés en rivière. Les trois chapitres abordés pour répondre à cette problématique sont: l'influence des travaux autoroutiers et de la fragmentation de l'habitat causée par les traverses sur les densités d'omble de fontaine (chapitre I), l'extension des modèles de dispersion dans des habitats fragmentés permettant une détection fine de l'effet des traverses sur les déplacements (chapitre II) et les modifications du nombre de sites de reproduction en fonction des étapes de construction autoroutière (chapitre III). Alors que le chapitre I dresse le patron global des impacts de l'autoroute sur les populations d'omble de fontaine, les chapitres II et III abordent des mécanismes possibles pouvant conduire au patron observé.

L'objectif du chapitre I a été d'évaluer les impacts des travaux autoroutiers (perte d'habitat par l'entremise de l'effet de la sédimentation) et de la présence des traverses autroutières (fragmentation par l'entremise de l'effet de barrière) sur les densités locales d'omble de fontaine. Compte tenu des connaissances actuelles sur le cycle de vie de l'omble de fontaine et des impacts des routes sur les écosystèmes aquatiques, les effets attendus étaient une réduction des densités en aval (facteur principal : construction) ou en amont (facteur principal : traverses). Nous avons utilisé un plan d'échantillonnage extensif de type BACI (Roedenbeck et al. 2007) et en palier (Walters et al. 1988) en suivant, au cours de trois étés consécutifs, les densités d'omble de fontaine dans 212 sections ouvertes de 25 m, réparties sur 35 cours d'eau le long de l'axe routier 73/175. La structure emboîtée des données a été prise en compte dans les effets aléatoires des modèles linéaires mixtes. Les effets fixes des modèles mixtes incluaient notamment des variables spatiales comme la localisation (amont et aval) ou la distance à l'axe routier (km), ainsi que des variables de traitement comme l'état d'avancement des travaux (avant, pendant et après) ou le type de traverse (niveau de franchissement faible, moyen et élevé). Les impacts de l'autoroute sur les densités d'omble de fontaine ont été évalués en comparant des modèles de plus en plus complexes, incluant différentes combinaisons d'interactions entre les variables spatiales et les variables de traitement.

L'objectif du chapitre II a été de développer un cadre de modélisation général décrivant la dispersion des poissons en présence d'obstacles, à partir de données de marquage – recapture. Ce cadre de modélisation inclut à la fois la façon dont les poissons se déplacent dans leur environnement (Rodríguez 2002, Coombs et Rodríguez 2007, Rodríguez 2010) et la façon dont les données sont récoltées sur le terrain (Hilborn 1990, Zurell et al. 2010). Les modèles ont été appliqués à des données de dispersion estivale d'omble de fontaine issues de quatre cours d'eau présentant des traverses représentatives de celles qui seront en place à la suite de l'élargissement de l'axe routier 73/175. Le niveau de franchissement des traverses a

été évalué par l'intermédiaire d'un paramètre de perméabilité inclus dans les modèles de dispersion (Rodríguez 2010). Le niveau de confiance de l'estimation de la valeur de ce paramètre a été validé par simulation (Zurell et al. 2010). Ce chapitre a examiné la dispersion comme une cause possible pouvant conduire aux patrons spatiaux observés au chapitre I (McIntyre et Fajardo 2009).

L'objectif du chapitre III a été de quantifier le retour des géniteurs sur les sites de reproduction suivant l'état d'avancement des travaux autoroutiers. L'effet attendu était une diminution des géniteurs sur les sites les plus affectés par la sédimentation (Whitman et al. 1982). Nous avons utilisé le dénombrement des nids comme mesure indirecte du nombre de géniteurs (Dauphin et al. 2010) et avons suivi la reproduction à proximité de l'autoroute pendant deux automnes consécutifs, sur 12 tronçons répartis sur un parcours linéaire de 115 km le long de l'axe routier 73/175. Les données ont été analysées suivant les analyses classiques proposées dans les expériences de type BACI (Green 1993). Si les effets de la sédimentation sur les stades de l'œuf à l'émergence sont bien documentés (Bernier-Bourgault and Magnan 2002, Jensen et al. 2009, Guillemette et al. 2011), l'investigation du retour des géniteurs sur des sites affectés par la sédimentation est plus rare (Whitman et al. 1982). Aussi, ce chapitre a examiné une cause encore peu explorée pouvant conduire à des modifications de la distribution spatiale des populations telles que mentionnées au chapitre I.

En plus d'acquérir des connaissances fondamentales sur la dynamique des populations de l'omble de fontaine en milieu fragmenté, la thèse a une composante appliquée visant à évaluer les impacts des travaux autoroutiers et des différents aménagements prévus pour faciliter le passage du poisson, dans une optique de gestion et de conservation des stocks de salmonidés en rivière.

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CHAPITRE I

IMPACTS OF HIGHWAY CROSSINGS ON DENSITY OF BROOK CHARR IN STREAMS

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Résumé

1. La dégradation de l'habitat et la fragmentation sont une préoccupation croissante en écologie. Pourtant la distinction entre les effets de ces deux processus peut être un défi difficile à relever. Dans les paysages fluviaux, les routes impactent les populations de poisson principalement par : (1) la restriction du passage des individus (fragmentation) et (2) la réduction de la qualité de l'habitat en aval par les augmentations de la charge sédimentaire (dégradation de l'habitat). Ces deux processus peuvent être différenciés pendant les projets de construction routière.

2. Cette étude examine les impacts d'une expansion autoroutière et la présence de traverses autoroutières existantes sur la densité de population locale d'omble de fontaine dans des tronçons de cours d'eau traversés par l'autoroute. La densité a été estimée durant trois étés consécutifs dans 212 sections distribuées parmi 36 cours d'eau. Ce plan d'échantillonnage extensif était axé sur la comparaison avec réplication des sites en amont et en aval des traverses autoroutières et incluait différents états d'avancement de la construction autoroutière (avant, pendant et après) et types de traverse autoroutière (niveau de franchissement faible, moyen et élevé). Les modèles mixtes ont été utilisés pour examiner les impacts de l'autoroute sur la densité de population locale.

3. Les activités de construction autoroutière n'ont pas eu d'effet détectable sur la densité. Toutefois, les traverses autoroutières existantes semblaient avoir un effet important sur la densité, laquelle différait sensiblement entre les sites en amont et en aval proche des traverses autoroutières dont le niveau de franchissement était moyen ou faible.

4. Un modèle de mouvement Markovien a produit des estimés du niveau de franchissement qui étaient cohérents avec la classification des types de traverse et a fourni des preuves sur la restriction du passage vers l'amont au niveau des traverses comme une explication plausible des différences observées dans la densité de population locale.

5. *Synthèse et applications*. La fragmentation de l'habitat résultant de la restriction du passage au niveau des traverses autoroutières a eu des effets sensiblement plus importants sur la densité de population locale que les impacts à court terme résultant des activités de construction. Les approches de modélisation utilisées dans cette étude peuvent être des outils de gestion utiles pour la conservation des espèces de poissons mobiles dans des paysages fluviaux fragmentés.

Mots-clés : barrière, connectivité, écologie des routes, évaluation des impacts environnementaux, marche aléatoire de Markov, modèles mixtes, mouvement, passage, poisson d'eau douce, ressources aquatiques

Summary

1. Habitat degradation and fragmentation are growing concerns in ecology, yet distinguishing between the effects of these processes can be a challenging task. In riverine landscapes, roads impact fish populations mainly through: (i) restriction of passage of individuals (fragmentation) and (ii) reduction in habitat quality downstream by increases in sediment load (habitat degradation). These two processes can be differentiated during road construction projects.

2. This study examines the impacts of a highway expansion and the presence of existing highway crossings on local population density of brook charr *Salvelinus fontinalis* in stream reaches traversed by the highway. Density was estimated on three consecutive summers in 212 sections distributed among 36 streams. This extensive sampling design focused on replicated comparison of sites upstream and downstream of highway crossings and included different stages of highway construction (before, during and after) and types of highway crossing (low, intermediate and high passability). Mixed models were used to examine the impacts of the highway on population density.

3. Highway construction activities had no detectable effect on density. However, existing highway crossings appeared to have a strong effect on density, which differed markedly between upstream and downstream sites near highway crossings of intermediate and low passabilities.

4. A Markovian movement model yielded estimates of passability that were consistent with the classification of crossing types and provided evidence for the restriction of upstream movement at crossings as a plausible explanation for observed differences in local population density.

5. *Synthesis and applications*. Habitat fragmentation resulting from restriction of passage at highway crossings had markedly greater effects on local population density than short-term impacts arising from construction activities. The modelling

approaches used in this study can be useful management tools for the conservation of mobile fish species in fragmented riverine landscapes.

Key-words: aquatic resources, barrier, connectivity, environmental impact assessment, freshwater fish, Markov random walk, mixed models, movement, passage, road ecology

Introduction

The reduction in connectivity caused by habitat fragmentation alters population dynamics and threatens the persistence of animal species (Fagan 2002; Fausch *et al.* 2002). Fragmentation *per se*, the breaking apart of formerly continuous habitat, must be distinguished from habitat loss, which reduces the amount of habitat remaining on the landscape; studies that confound these two processes can produce misleading results (Fahrig 2003).

Although distinguishing fragmentation from habitat loss is often difficult in practice, habitat loss is viewed as a more important driver of species distribution patterns than fragmentation in terrestrial landscapes (Fahrig 2003; Mortelliti *et al.* 2011). In riverine landscapes, these two processes can be differentiated during road construction projects. Roads are one of the main sources of anthropogenic fragmentation; they are associated with losses of both connectivity and habitat extent and can have major ecological impacts (Trombulak & Frissell 2000; Allan 2004; Wheeler, Angermeier & Rosenberger 2005). Some effects of roads such as alteration of physical and chemical environments, reduction in habitat connectivity and increased mortality for animal species occur both in aquatic and terrestrial ecosystems. However, effects such as mortality caused by sediments and pollutants can be spatially asymmetrical in riverine landscapes because they occur predominantly downstream of the road (Fig. S1, Supporting Information). Sedimentation (particularly during road construction, habitat degradation or loss) and obstructions to fish passage (road-crossing structures, fragmentation) are the two main environmental impacts leading to differences in fish density and distribution near roads (Wheeler, Angermeier & Rosenberger 2005). In rivers and streams, fish are subject to a range of impacts resulting from increased sediment loading from anthropogenic activity (Waters 1995; Kemp *et al.* 2011). Reduction in survival to emergence through the accumulation of fine sediments in the substrate has been well

documented for fish species (reviewed in Kemp *et al.* 2011), including salmonids (Jensen *et al.* 2009; Guillemette *et al.* 2011). By reducing the abundance and availability of benthic invertebrates, fine sediment transport and deposition can also reduce the summer growth and survival of fish (Suttle *et al.* 2004; Harvey & Railsback 2009). Fish densities downstream of a road may therefore be reduced as a consequence of fine sediment loading. The presence of road crossings may also reduce the connectivity of the riverine landscape and thus be detrimental to viability of fish populations (Schick & Lindley 2007; Bouska & Paukert 2010). Fish may have difficulties moving through instream structures at road crossings during low summer flow (Warren & Pardew 1998) or spawning migrations (Belford & Gould 1989), and these barrier effects are often related to the type of structure built at the crossing (Warren & Pardew 1998).

The highway between Quebec and Saguenay cities (Quebec, Canada) was built in 1948. A major construction project, undertaken during the period 2006–2012, widened the highway from two to four traffic lanes. The mean width of the highway's 'zone of influence', which includes the traffic lanes and all areas required for road security and maintenance, such as ditches and additional strips of land, increased from 30 to 120 m. The measures implemented to reduce sedimentation during construction included the use of erosion control mattresses to stabilise stream banks, gravel filters placed along construction ditches to promote sedimentation and geotextile curtains to limit dispersal of suspended particulate matter. Brook charr *Salvelinus fontinalis*, which is found in almost all of the streams crossed by the highway, can be affected both by sediment loading (Guillemette *et al.* 2011) and facilities for fish passage at road crossings (Belford & Gould 1989). This system therefore provides a suitable model for evaluating the influence of habitat degradation and fragmentation on brook charr populations.

Environmental impacts often occur at different spatio-temporal scales, creating challenges for study design and statistical analysis (Stewart-Oaten & Bence 2001). One of the main difficulties is to isolate human-made disturbance from natural variation of the studied phenomenon (Walters, Collie & Webb 1988). The before-after-control-impact (BACI) approach and its derivates have been the most commonly used sampling designs in environmental impact assessments (Stewart-Oaten & Bence 2001). However, BACI designs have been criticised for lacking replication and not discriminating effectively between variation within and between control and treatment units (Murtaugh 2000), and for not taking into account the correlation structure of nested observations (McDonald, Erickson & McDonald 2000). When more than a single impacted site is available for inclusion in the study, multiple BACI (MBACI) designs, which compare a group of impacted sites to a group of control sites, can be used to address the issue of replication (Downes *et al.* 2002; Angeler & Moreno 2007).

The present study aims to investigate the potential impacts of highway construction (habitat degradation through sedimentation) and the presence of existing highway crossings (fragmentation through barrier effects) on brook charr density. Our analysis is based on spatially extensive sampling, over a 3-year period, of brook charr density at sites upstream and downstream of the highway. The major strengths of our design are that (i) treatment temporal trajectories have adequate replication; (ii) the initiation of construction treatments is staggered in time (the 'staircase' design of Walters, Collie & Webb 1988), thus controlling for time–treatment interactions; (iii) intra-group correlations arising from nested sampling are accounted for by random effects in mixed model analyses.

Specifically, we tested whether differences between local population densities at upstream and downstream sites were affected by two treatments: stage of highway construction and type of highway crossing. We tested the hypotheses that (i)

construction effects operating over the time scale covered by the study (3 years or shorter) cause differences in density to increase following the initiation of construction; (ii) if existing highway crossings act as long-term barriers to passage, differences in density will be linked to structural features that determine passability of the crossing. We also developed a Markovian random walk model allowing for differences in barrier passability and directional bias in fish movements and examined its behaviour at equilibrium to examine whether restriction of passage at crossings can explain observed differences in local density.

Materials and methods

Study system and data collection

The study was conducted along a 157-km stretch of the highway in the Jacques-Cartier National Park and the Laurentides Wildlife Reserve, located on the Laurentian Plateau at altitudes between 190 and 820 m (Fig. 1). The area has a humid continental climate with harsh winters (mean annual temperature: 0·3 °C; annual snowfall: 639 cm). Vegetation cover is continuous boreal forest dominated by balsam fir *Abies balsamea* and white birch *Betula papyrifera*. Watershed geology is largely homogeneous and consists of a metamorphic basement (gneiss) with intrusive rocks (mainly mangerites); stream formation is primarily by glacial deposits and outwash. The annual discharge regime has a dominant peak in the spring at snowmelt and seasonal lows in late summer. The highway is the only conspicuous source of human disturbance on the aquatic environment.

Brook charr density (100^{-1} m^{-2}) was estimated in 3 consecutive years (2006-2008) at 212 stream sections distributed among 37 reaches in 36 streams (Strahler order 1–3, median length = 3·0 km and median slope = 4·4%) crossed by the highway (Fig. 2). The portion of total stream length spanned by the reaches ranged from 0·6 to

77·6% (median = 22·8%). Reaches were randomly assigned a rank (1–37) and were visited in the sequence determined by rank order from mid-June to late August in 2006 (37 reaches, 206 sections), 2007 (36 reaches, 198 sections) and 2008 (34 reaches, 187 sections). Brook charr were sampled by single-pass electrofishing (Smith-Root D-15, Vancouver, WA, USA) in an upstream direction within open stream sections (Jones & Stockwell 1995). Voltage and waveform were adjusted as required to account for variation in water conductivity. Stream width (m) was measured at five transects spaced equally along each section. Sections were 25 m in length (mean section width = 3·9 m and mean section area = 96·2 m^2). Habitat management during the construction period (nine reaches) involved restoration of natural pool and riffle habitats within the first 100 m upstream or downstream of the highway. No major modifications to crossings (e.g. concrete aprons and baffles) were present in any of the reaches. Pools immediately downstream of the highway were avoided when selecting the study sections. Captured fish were counted, measured (total length, TL) and released at their section of origin.

Brook charr were present in all 37 reaches and accounted for 91·9% (10 653 individuals) of all fish captured. Longnose dace *Rhinichthys cataractae* (4·5%), Atlantic salmon *Salmo salar* (1·8%), white sucker *Catostomus commersoni* (0·3%), longnose sucker *Catostomus catostomus* (0·1%) and small unidentified cyprinids (1·4%) were also present in the streams. Brook charr were relatively small (TL: median = 65 mm; 1st quartile = 50 mm; 3rd quartile = 96 mm) and young (54·9% in the young-of-the-year age group).

Statistical analyses

We used linear mixed models to account for the hierarchical structure of the sampling design, which had sections nested within reaches and repeated observations

nested within sections (Wagner, Hayes & Bremigan 2006; Deschênes & Rodríguez 2007). All mixed models had the following general structure:

$$Y_{srt} = \alpha_0 + \alpha_1\, Year_{2007} + \alpha_2\, Year_{2008} + \alpha_3\, Width_{srt} + \beta_j\, X_{jsrt} + \varepsilon_{srt} + u_{sr} + v_r$$

where Y_{srt} is brook charr density transformed as $\log_e(x + 1)$, the X_{jsrt} is p variables associated with treatment effects and spatial location as described below, α_i ($i = 0,\ldots,$ 3) and β_j ($j = 1, \ldots, p$) are coefficients and the remaining indices represent section (s), reach (r) and sampling year (t). The first five terms on the right-hand side of the equation represent the systematic component of the model. $Year_{2007}$ and $Year_{2008}$ are categorical covariates coded as (−1, −1), (1, 0) and (0, 1) for years 2006, 2007 and 2008, respectively. *Width* is a continuous covariate, mean stream width, transformed as $\log_e(x)$ and standardised. The last three terms on the right-hand side of the equation represent the random component of the model. The u_{sr} and v_r terms represent random effects for section and reach, respectively, and ε_{srt} is random error. All random terms are assumed to follow a normal distribution with zero mean and variance to be estimated.

Two types of treatment effect were considered: stage of highway construction and type of highway crossing. Three alternative classification schemes based on the durations of both construction and recovery after construction and denoted here as C1, C2 and C3, were used to characterise the stage of construction of individual reaches (Fig. S2, Supporting Information). Type of highway crossing (H) was classified according to passability as high (21 reaches), intermediate (10 reaches) or low (6 reaches) (Fig. 3). To assess passability, we modified a classification system previously used by Love & Taylor (2003) and Poplar-Jeffers *et al.* (2009) to classify culverts in trout streams. The modifications we introduced account for features specific to our study system (e.g. presence of bridges and spillway design). Specifically, we (i) used the presence of a bridge at the crossing, rather than

occurrence of streambed substrate in a culvert, as our first criterion for branching; (ii) did not use descriptors of the culvert inlet or channel width and (iii) assumed that control structures (spillways with natural substrate) ensured high passability; the unmodified classification assumes that weirs and baffles lead to intermediate passability. Dummy indicators were used to code both construction (reference category: 'Before construction') and highway crossing (reference category: 'High passability'). Reaches 122·39 and 212·16, initially classified as having intermediate passability, were classified as highly passable after modifications from highway construction activities in 2008 and 2007, respectively. Spatial location of sections was represented by two variables: position relative to the highway, P, coded as a binary indicator: upstream (0) or downstream (1) and distance from the highway, D (km, negative distances upstream and positive distances downstream from the highway).

We built a sequence of increasingly complex models including various additive combinations of treatment and location variables, as well as interactions between these variables (Table 1). The interaction terms between position and treatment indicate whether differences between local population densities at upstream and downstream sites are influenced by the treatment; such interactions are therefore viewed as instrumental in detecting environmental impacts (Underwood 1994). The set of models considered allows for the detection of a broad variety of potential effects on densities. Model comparison was based on Akaike Information Criterion adjusted for sample size, AIC_c (Burnham & Anderson 2002). Models were ranked using ΔAIC_c, the difference in AIC_c between a candidate model and the model with the lowest (best) AIC_c. Parameter estimation was based on a full maximum likelihood procedure. All analyses were carried out in the R environment (R Development Core Team 2010; nlme package, v. 3.1-96).

We used a Markovian random walk model (Appendix S1, Supporting Information) to assess whether longitudinal fish movements and responses to barriers

were a plausible explanation for the spatial patterns in density revealed by the linear mixed models. The model applies to a fish population in an idealised stream reach separated into upstream and downstream portions by a potential barrier located at the mid-point of the reach. Our approach extends the simple random walk by allowing barrier effects and directional bias to influence movements. Key model assumptions are as follows: (i) movement behaviours, including responses to a barrier, are density-independent, constant in time and identical across individuals; (ii) population size and spatial distribution are at equilibrium; (iii) fish follow a random walk that may be biased towards upstream or downstream movement; (iv) barriers do not hinder downstream movement but may affect upstream movement of fish that encounter them. We used a least-squares procedure to fit the Markovian model to density estimates derived from the linear mixed models (Appendix S1, Supporting Information). This procedure yielded point estimates and standard errors for four parameters that defined the transition matrix of the Markov chain: barrier passabilities for the three types of crossing (high, intermediate and low) and probability of downstream movement.

Results

The comparison of models incorporating different classification schemes to represent stage of construction (Fig. S2, Supporting Information) indicated that scheme C3 outperformed schemes C1 and C2; therefore, the results for models accounting for the stage of construction are presented only for models based on scheme C3. Model fit was improved by inclusion of variables representing position relative to the highway and distance from the highway (Table 1), but further inclusion of stage of construction (scheme C3; models 6–8) led only to marginal improvement in fit. The best fits were obtained for models including position relative to the highway, distance from the highway and type of crossing. More specifically, the best-fitting model in the candidate set (model 12) included interactions between position

and type of crossing, position and distance, and type of crossing and distance (Tables 1 and 2). Graphical comparison of observed densities with those estimated from model 12 revealed that the model provided a reasonable fit and showed no obvious departures from the statistical assumptions of linearity and constant residual variance (Fig. S3, Supporting Information).

Parameter estimates from model 12 (Table 2) were used to display graphically the joint effect of position, type of highway crossing and distance from the highway on density (Fig. 4). Density seemed mostly unaffected by position and distance from the highway for highway crossings having high passability (Fig. 4). In contrast, markedly different relationships between density and distance from the highway were found on either side of the highway for crossings of intermediate and low passability, leading to sharp discontinuities in estimated densities near the highway crossing (Fig. 4). In the vicinity of the highway (distance *c.* 0 m), the ratio of downstream to upstream densities was estimated as *c.* 7 for crossings of intermediate passability and *c.* 34 for crossings of low passability. Averaged over the upstream and downstream portions of the reach (0·8 km to either side of the crossing; Fig. 4), the ratio of downstream to upstream densities was estimated as *c.* 2 for crossings of intermediate passability and *c.* 6 for crossings of low passability.

The Markovian random walk model was a good fit to density estimates from the linear mixed model (Fig. 4). Parameter estimates (standard error in parentheses) for barrier passabilities for the three types of crossing (low, k_L; intermediate, k_I and high, k_H) (Appendix S1, Supporting Information) were $k_L = 0{\cdot}043$ (0·0026), $k_I = 0{\cdot}186$ (0·0044) and $k_H = 0{\cdot}645$ (0·0122). These estimates indicate a decline in probability of passage for all crossing types; reduction in passability relative to a perfectly permeable barrier ($k = 1$; Rodríguez 2010) ranged from *c.* 35% for crossings of high passability to >95% for crossings of low passability. The estimate for the probability of downstream movement, $p_d = 0{\cdot}488$ (0·0002) pointed to an overall

directional bias towards upstream movement. The Markov model applies to an equilibrium situation (as described by the stationary distribution of the chain), and so this estimate represents a long-term value that averages over seasonal and yearly variations. Directional bias was required for the Markov model to generate the observed spatial discontinuities in density. Simulations for different values of k showed that the observed curvilinear gradients in density were not generated from a spatially homogeneous initial distribution in the absence of directional bias, that is, when $p_d = 0{\cdot}5$.

Discussion

Effects of highway contruction

We did not detect an effect of highway construction activities on brook charr density downstream of the highway. Increased sedimentation is the most common impact affecting stream fish following road construction (Trombulak & Frissell 2000; Wheeler, Angermeier & Rosenberger 2005). The hydrological network can be particularly altered at intersections with roads, resulting in higher peak flows and sedimentation in downstream reaches (Jones *et al.* 2000). Sediment loading arising from road construction has been shown to be related to the stage of construction mostly along the first kilometre downstream of the source of sediments (Lachance *et al.* 2008). Highway construction activities were the only known supplemental source of sediments in our study, and sediment-induced turbidity was apparent in some reaches, yet the models incorporating the stage of highway construction did not reveal any substantial impact of sediment loading on brook charr densities. Newcombe & MacDonald (1991) suggested that both intensity and duration of exposure to suspended sediments must be known to predict the impacts of sedimentation on aquatic ecosystems. However, intensity of sediment loading alone is

a poor predictor of impacts of suspended sediment (Newcombe & MacDonald 1991), and accurate quantification of sediment loading *in situ* is costly and time-consuming.

Different hypotheses could explain why highway construction activities had no apparent impact on brook charr density. First, measures taken to mitigate sediment loading into the streams during construction may have sufficed to prevent any impact on brook charr density. Secondly, most analyses of the effect of sediment on salmonids are from laboratory or field experiments focusing on growth and survival of juveniles (Suttle *et al.* 2004), or field studies focusing on embryonic stages (Guillemette *et al.* 2011). However, the responses at the population level might be different from those at embryonic and juvenile stages. For example, Curry & MacNeill (2004) showed that density of brook charr did not decrease in response to sedimentation, although survival to emergence was reduced.

In contrast to the long-term effects of highway crossings, which in our study system have been in place since 1948, the effects of suspended sediments can be short-lived if the stream has sufficient power to flush the material rapidly. Sub-lethal short-term responses of fish to increased sediment loads include behavioural avoidance (Scrivener, Brown & Andersen 1994), increased movement (Bergstedt & Bergersen 1997) and changes in physiology, foraging and growth (Harvey & Railsback 2009). Our design limits the detection of construction effects to those manifested within at most a 3-year period. Longer-lived latent effects of deposited sediment (Harvey & Railsback 2009) may therefore have gone undetected.

Effets of highway crossings

Brook charr populations were affected by highway crossings, as shown by differences in local density between upstream and downstream sites in the vicinity of highway crossings of intermediate and low passabilities. The slope of highway

crossings and the presence of an outlet drop appear to be the most important predictors of passability (Love & Taylor 2003; Poplar-Jeffers *et al.* 2009). These two factors are often cited as causes of obstruction to free movement of fish and are widely considered in management policies (Warren & Pardew 1998; Poplar-Jeffers *et al.* 2009).

It seems unlikely that the observed density gradients were driven by differences in local habitat (e.g. through congregation of fish in plunge pools below the crossings), because habitats near the crossings were in a relatively natural state and fish were not collected in or very near to pools immediately downstream of crossings (Materials and methods: study system and data collection). Furthermore, larger pools tended to be associated with highly passable crossings such as wide bridges.

The Markov model produced results that were consistent with the observed patterns in density and provided insight into potential processes (barrier effects coupled with upstream movement) that could parsimoniously explain these patterns. The Markov model also provided quantitative estimates of passability that were consistent with the classification of crossing types and pointed to a decline in probability of passage for all crossing types. The apparent reduction in passability at crossings classified as highly passable is perhaps surprising in view of the known upstream swimming ability of brook charr (Adams, Frissell & Rieman 2000). However, lack of an attempt to pass a structure may result not from inability to pass, but from lack of motivation to pass after encountering the barrier (Kemp & O'Hanley 2010). Furthermore, swimming ability is strongly size-dependent and small brook charr (< 100 mm) may move less frequently and be inhibited by obstacles more readily than larger fish (Adams, Frissell & Rieman 2000). Brook charr populations in our study comprised mostly small juvenile fish (77% had TL < 100 mm); our results may therefore not generalise to populations of larger individuals.

Both the relative surplus (downstream) and deficit (upstream) of density near the crossing and the directional movement bias quantified by the Markov model are consistent with the notion that reduced passability affected primarily upstream movements (Morita, Yamamoto & Hoshino 2000). Telemetric tracking and length-frequency distributions indicate that in this system, spawners move readily between lakes and streams for at least some of the streams and suggest that the extent to which reproductive strategies involve migration, partial migration or residency may vary as a function of hydrological features such as distance from the stream spawning sites to the nearest lake. If the directional bias indicated by the Markov model truly reflects a stable, long-term pattern of movement, it would raise the intriguing possibility that brook charr populations in these small streams are at least partly sustained or supplemented by immigration from downstream source populations. A plausible scenario is that longitudinal differences in juvenile density arise when crossings restrict the upstream migration of spawners originating from downstream sources, and the spatial distribution of juvenile fish subsequently reflects the distribution of spawners during the spawning period. Such residual effects of spawning site location on the distribution of juvenile fish are well documented in stream salmonids (Hudy *et al.* 2010; Tentelier & Piou 2011). Alternatively, longitudinal differences in density could be generated primarily by upstream movement of young-of-the-year fish. Young brook charr sometimes show preferential upstream movement during the summer (Adams, Frissell & Rieman 2000; Peterson & Fausch 2003). However, mark–recapture trials conducted in four of the study streams showed no evidence of directional bias in brook charr movements during the summer (M. Pépino, M.A. Rodríguez & P. Magnan; unpublished data).

Density estimates derived from one-pass electrofishing are potentially subject to various sampling biases. In the present study, the use of random effects at the reach and section levels in the mixed models presumably helped to control for nuisance effects of unmeasured covariates on density (Gilks *et al.* 1993). Habitat features that

influence the efficacy of electrofishing, such as stream width, conductivity, stream gradient and fish size distribution (Hense, Martin & Petty 2010), were relatively homogeneous within reaches (Table S1, Supporting Information), suggesting that variation in capture efficiency among sites did not unduly affect observed longitudinal patterns in density.

Management implications and conclusions

Restriction of fish passage at highway crossings and concomitant declines in stream connectivity (fragmentation) had markedly greater effects on local population densities than short-term impacts arising from construction activities (habitat degradation). These results contrast with the findings of many studies in terrestrial landscapes showing that habitat loss, rather than habitat fragmentation *per se*, is a main driver of distribution patterns (Mortelliti *et al.* 2011). Our results support the notion that highway crossings can contribute to fragmentation of the riverine landscape, with potential impacts on population persistence of stream fish (Letcher *et al.* 2007).

Density differences upstream and downstream of crossings may have implications for individual fitness of fish near the crossings. At densities similar to those in our study system, individual growth and energy acquisition for a population of brook charr have been shown to be density-dependent during warm periods (Utz & Hartman 2009). Sharp density differences were generated by the Markov model through processes that do not depend on local habitat quality. This result adds to a long list of caveats that density may be a misleading indicator of habitat quality (Van Horne 1983) and illustrates that explicit consideration of movement can sometimes help to avoid this pitfall (Bélanger & Rodríguez 2002). In this context, development of dispersal models that account for fragmentation in riverine landscapes (e.g. Schick & Lindley 2007; Rodríguez 2010) can contribute to a better understanding of

biological processes underlying the observed spatial patterns (McIntire & Fajardo 2009).

Small tributaries are key rearing and spawning habitats for most salmonid species (Curry, Sparks & Van De Sande 2002); therefore, estimating habitat suitability upstream from barriers to determine the amount of habitat rendered unavailable by restriction of passage is an important goal for wildlife managers (Poplar-Jeffers *et al.* 2009). The decline of local densities upstream of crossings of intermediate and low passabilities provides a quantitative estimate of habitat loss resulting from reduction in connectivity. Our approach is therefore complementary to molecular approaches used to assess impacts of barriers (Wofford, Gresswell & Banks 2005; Griffiths *et al.* 2009), which highlight the genetic isolation of populations and provide information on changes in effective population size rather than local population density.

Explicit modelling of barriers to passage is a valuable management tool for the conservation of mobile fish species in fragmented riverine landscapes. Managers can use the modelling approaches proposed in this study to evaluate the impact of different crossing structures and the uncertainty associated with the resulting estimates. Estimates of impact derived from the models can inform decisions about construction of new barriers and prioritization for mitigation schemes or barrier removal. We emphasise that the evaluation of alternative structures needs not be based on discrete crossing types, because mixed models allow for a more nuanced characterisation of crossings by combining multiple descriptors, both continuous and discrete.

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Table 1. Comparison of 12 candidate models differing in their systematic component. The deviance, number of model parameters (K), adjusted Akaike Information Criterion (AIC_c) and difference in AIC_c relative to the best-fitting model (ΔAIC_c) are presented. Model terms are C3, stage of highway construction ('before', 'during' or 'after' construction; Fig. S2c, Supporting Information); H, type of highway crossing ('low', 'intermediate' or 'high' passability; Fig. 3; P, position relative to the highway ('upstream' or 'downstream'); D, distance from the highway

Model	Terms in systematic component of model*	Deviance	K	AIC_c	ΔAIC_c
1	Constant (α_0), year and stream width	1 500	7	1 515	56
2	P	1 481	8	1 497	38
3	D	1 492	8	1 509	50
4	P + D	1 477	9	1 496	37
5	P + D + P x D	1 476	10	1 496	37
6	P + C3 + P x C3	1 472	12	1 497	38
7	P + C3 + P x C3 + D	1 468	13	1 495	36
8	P + C3 + P x C3 + D + P x D	1 466	14	1 495	36
9	P + H + P x H	1 442	12	1 466	7
10	P + H + P x H + D	1 440	13	1 467	8
11	P + H + P x H + D + P x D	1 432	14	1 461	2
12	P + H + P x H + D + P x D + H x D	1 426	16	1 459	0

*All models include a constant term (α_0), categorical covariates coding for year, mean stream width (m; standardized after $\log_e$-transform), and random terms for stream, section and error.

Table 2. Parameter estimates for the best overall model (Table 1: model 12) of brook charr density. The dependent variable is brook charr density, transformed as $\log_e(x+1)$. Estimates and confidence intervals for the systematic and random components are presented. The σ^2 terms represent variances of random terms for error ($\sigma^2_{\varepsilon_{srt}}$), section ($\sigma^2_{u_{sr}}$) and reach ($\sigma^2_{v_r}$)

		95% confidence intervals	
	Estimate	Lower	Upper
Systematic component			
Constant (α_0)	2.757	2.279	3.235
Year			
$Year_{2007}$	0.127	0.055	0.198
$Year_{2008}$	0.136	0.063	0.209
Mean stream width ($\log_e(x)$; standardized)	-0.557	-0.703	-0.411
Position (reference: upstream)	0.023	-0.446	0.491
Highway crossing (reference: high passability)			
Intermediate passability	-1.260	-1.902	-0.618
Low passability	-2.021	-3.127	-0.916
Distance (km)	0.913	-0.098	1.925
Distance x Position	-1.244	-2.602	0.113
Distance x Highway crossing			
Distance x Intermediate passability	-1.726	-3.666	0.214
Distance x Low passability	-2.152	-3.964	-0.340
Position x Highway crossing			
Position x Intermediate passability	1.666	0.828	2.504
Position x Low passability	2.879	1.866	3.893

Table 2. (Continued)

	Estimate	95% confidence intervals	
		Lower	Upper
Random component			
$\sigma^2_{\varepsilon_{srt}}$	0.611	0.569	0.657
$\sigma^2_{u_{sr}}$	0.515	0.435	0.609
$\sigma^2_{v_r}$	1.026	0.790	1.331

Figure legends

Figure 1. Map showing the position of the 37 study reaches along the 73/175 highway (Quebec, Canada). The intensity of shading is proportional to altitude.

Figure 2. Schematic representation of the distribution of 212 stream sections (vertical tick marks) among 37 reaches (horizontal lines). Reaches are identified by milepost distance from south (km 64·70) to north (km 221·60). Distances from the highway are provided along the bottom scale for the upstream (negative values) and downstream (positive) sections of each reach. Strahler stream order is provided for each reach.

Figure 3. Decision tree for classification of highway crossings, modified from Love & Taylor (2003) and Poplar-Jeffers *et al.* (2009). Each highway crossing structure is classified by passability as high, intermediate or low.

Figure 4. Estimated fish density (solid lines) and 95% confidence intervals (shaded areas) as a function of distance from the highway and passability type (high, intermediate and low; Fig. 3), for the best-fitting linear mixed model (Table 1: model 12). Estimated fish density derived from the Markovian movement model (Appendix S1, Supplementary Information) is also shown (broken lines). Distances from the highway are provided along the bottom scale for upstream (negative values) and downstream (positive) sections.

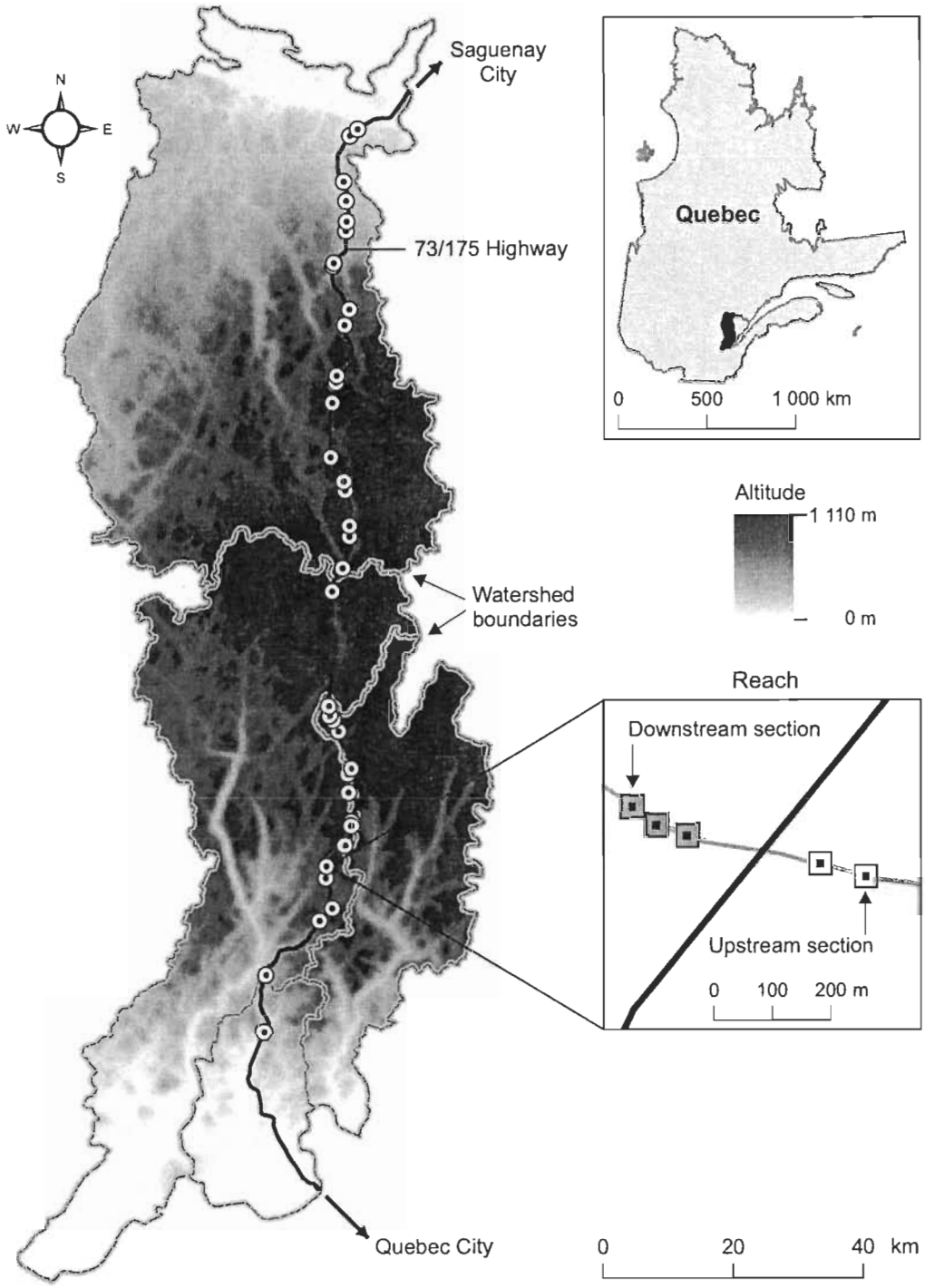
N
W
E
S
Saguenay City
73/175 Highway
Watershed boundaries
Quebec City
Quebec
0 500 1 000 km
Altitude
1 110 m
0 m
Reach
Downstream section
Upstream section
0 100 200 m
0 20 40 km

Figure 1

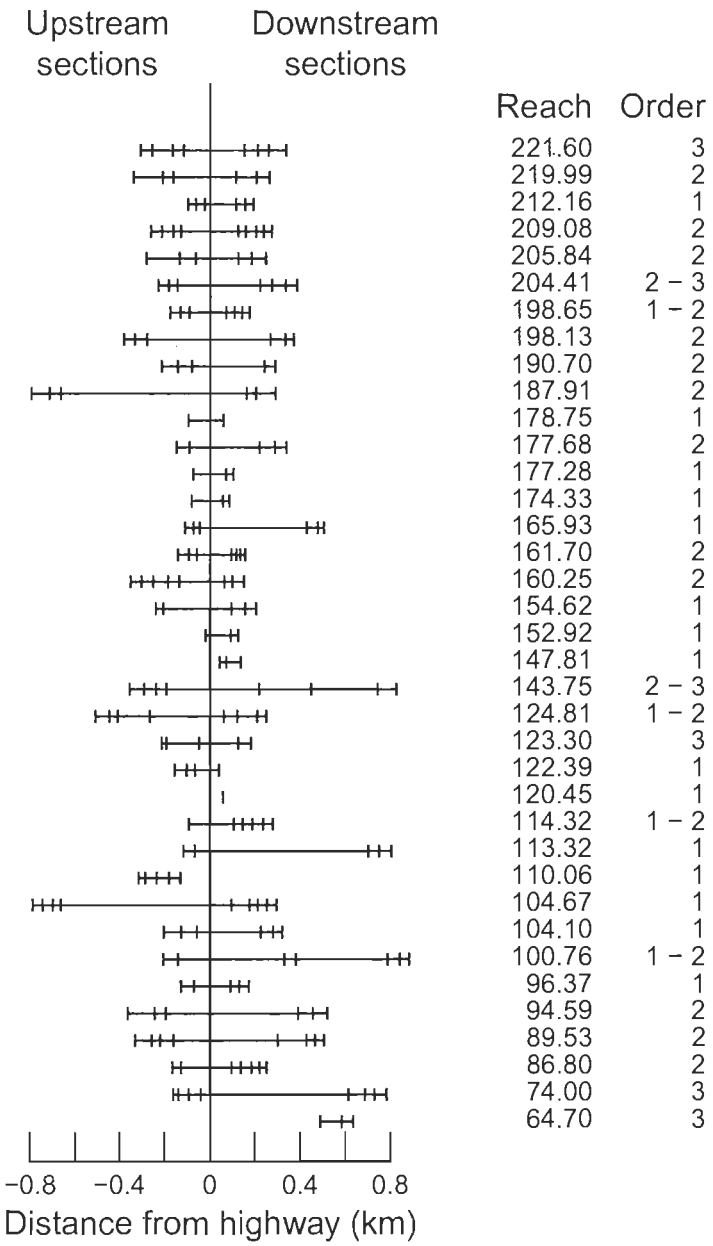
Upstream sections
Downstream sections
Reach Order
221.60 3
219.99 2
212.16 1
209.08 2
205.84 2
204.41 2 – 3
198.65 1 – 2
198.13 2
190.70 2
187.91 2
178.75 1
177.68 2
177.28 1
174.33 1
165.93 1
161.70 2
160.25 2
154.62 1
152.92 1
147.81 1
143.75 2 – 3
124.81 1 – 2
123.30 3
122.39 1
120.45 1
114.32 1 – 2
113.32 1
110.06 1
104.67 1
104.10 1
100.76 1 – 2
96.37 1
94.59 2
89.53 2
86.80 2
74.00 3
64.70 3
−0.8 −0.4 0 0.4 0.8
Distance from highway (km)

Figure 2

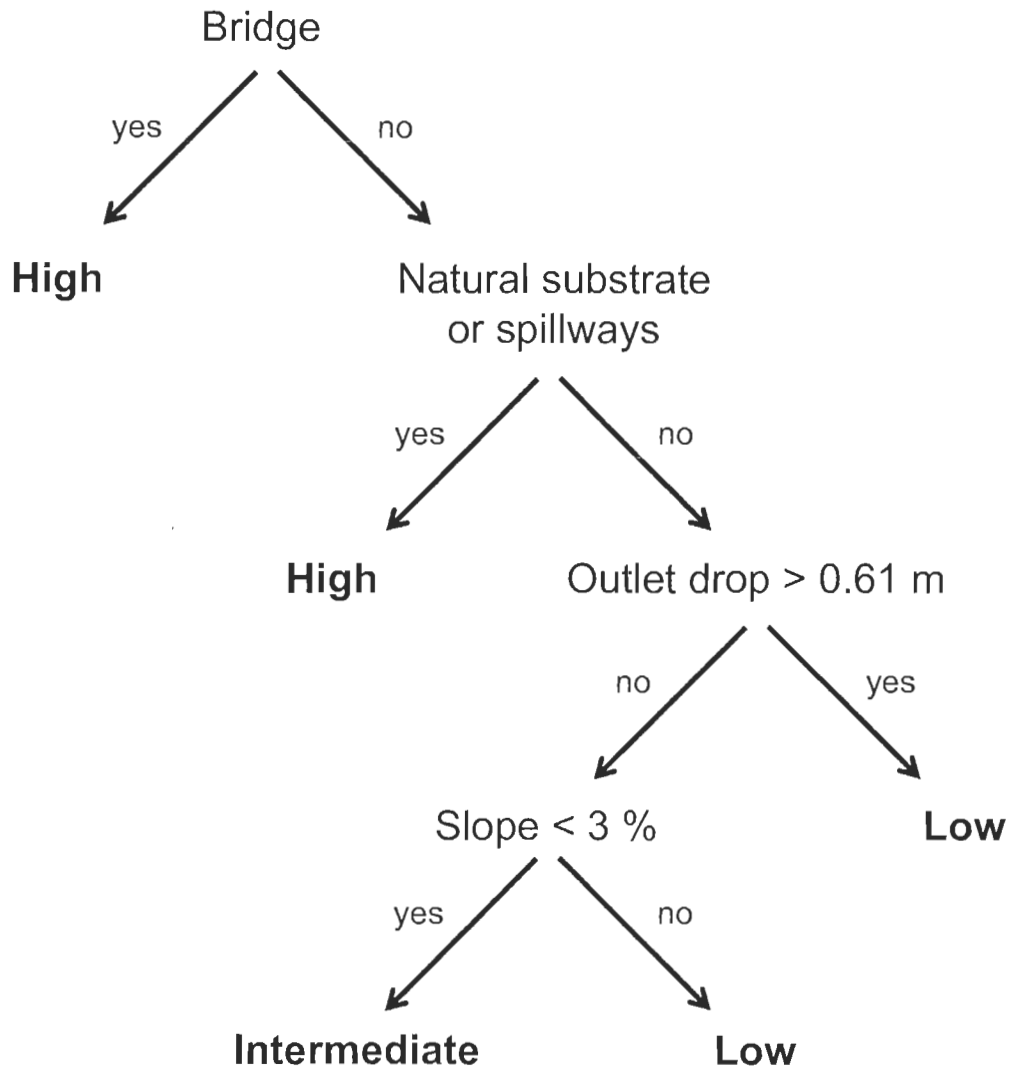
Bridge
yes
no
High
Natural substrate or spillways
yes
no
High
Outlet drop > 0.61 m
no
yes
Slope < 3 %
Low
yes
no
Intermediate
Low

Figure 3

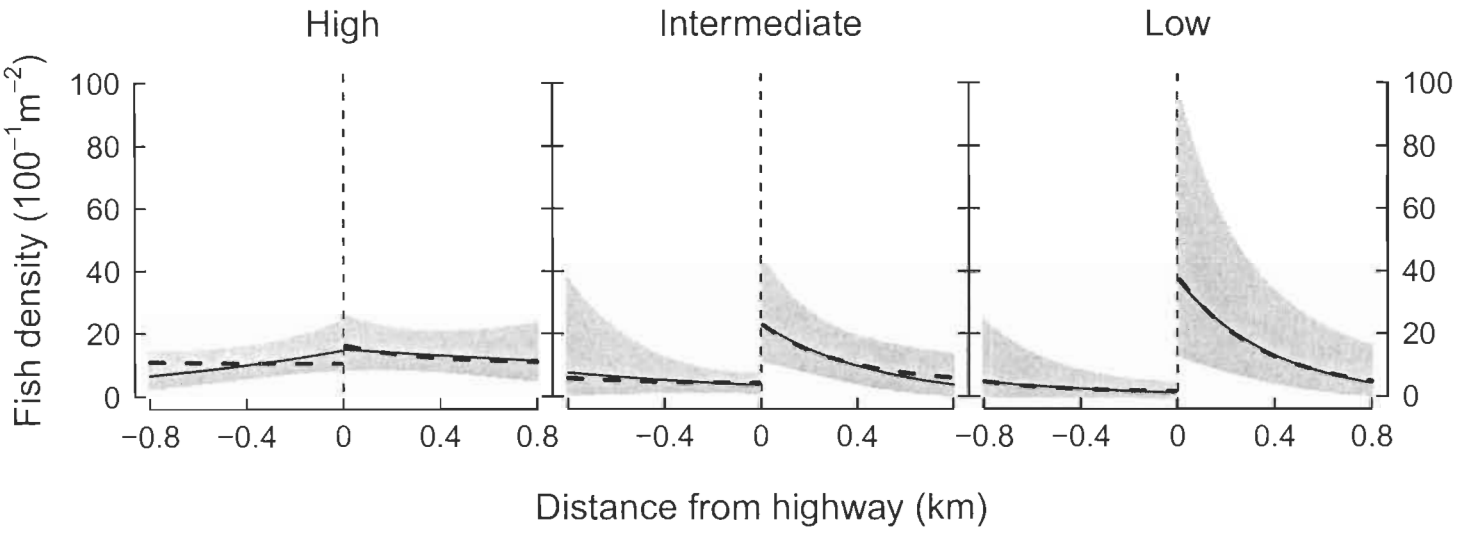
High
Intermediate
Low
Fish density ($100^{-1}m^{-2}$)
100
80
60
40
20
0
−0.8
−0.4
0
0.4
0.8
Distance from highway (km)

Figure 4

Supporting Information

Table S1. Summary statistics for fish body length and environmental characteristics of study reaches upstream and downstream of highway crossings. For each variable, means were calculated separately for the upstream and downstream portions of each reach; the medians (25% – 75% quartiles) of those means are reported

Variable	Upstream	Downstream
Mean fish length (mm)	85.4 (78.7 – 100.5)	76.5 (59.2 – 86.4)
Mean stream width (m)	2.6 (1.6 – 5.0)	3.4 (2.1 – 5.3)
Mean stream depth (m)	0.28 (0.17 – 0.39)	0.32 (0.22 – 0.40)
Mean conductivity (μS/cm)	18 (7 – 78)	91 (35 – 159)
Mean slope (%)	4.6 (2.9 – 5.7)	4.0 (2.9 – 5.2)

Supporting Information

Figure S1. Road impacts on wildlife populations (modified from Jaeger & Fahrig 2004). a) Road avoidance and mortality from collisions are the two main impacts of roads on terrestrial populations. b) In streams and rivers, mortality caused by sediments and pollutants originating from the road should occur predominantly downstream. Initial migrants can arrive from either side of the road.

Figure S2. Stages of highway construction in 2006, 2007, and 2008. The number of reaches is given as totals per year (n) and by stage of construction (within symbols). White symbols: before construction; grey symbols: after construction; black symbols: during construction.

Figure S2a. Scheme C1: symbols represent eight possible stages of highway construction ("before construction", "first year of construction", "second year of construction", "second year of construction - construction interrupted for one year", "third year of construction", "first year after construction - construction lasted one year", "second year after construction - construction lasted one year", "first year after construction - construction lasted two years").

Figure S2b. Scheme C2: coding simplified from C1 by omitting the duration of construction. Symbols represent five stages of highway construction ("before construction", "during construction", "first year after construction - construction lasted one year", "second year after construction - construction lasted one year", "first year after construction - construction lasted two years").

Figure S2c. Scheme C3: coding simplified from C1 by omitting the durations of both construction and recovery after construction. Symbols represent three stages of highway construction ("before", "during", and "after" construction).

Figure S3. Model fit (estimated vs. observed fish density) for the best overall linear mixed model (Table 1: model 12). Plots are for individual reaches, grouped according to passability (a through c). Reach milepost distances (Fig. 2) are shown above each plot. One-to-one (dotted) and ordinary regression (solid) lines are shown.

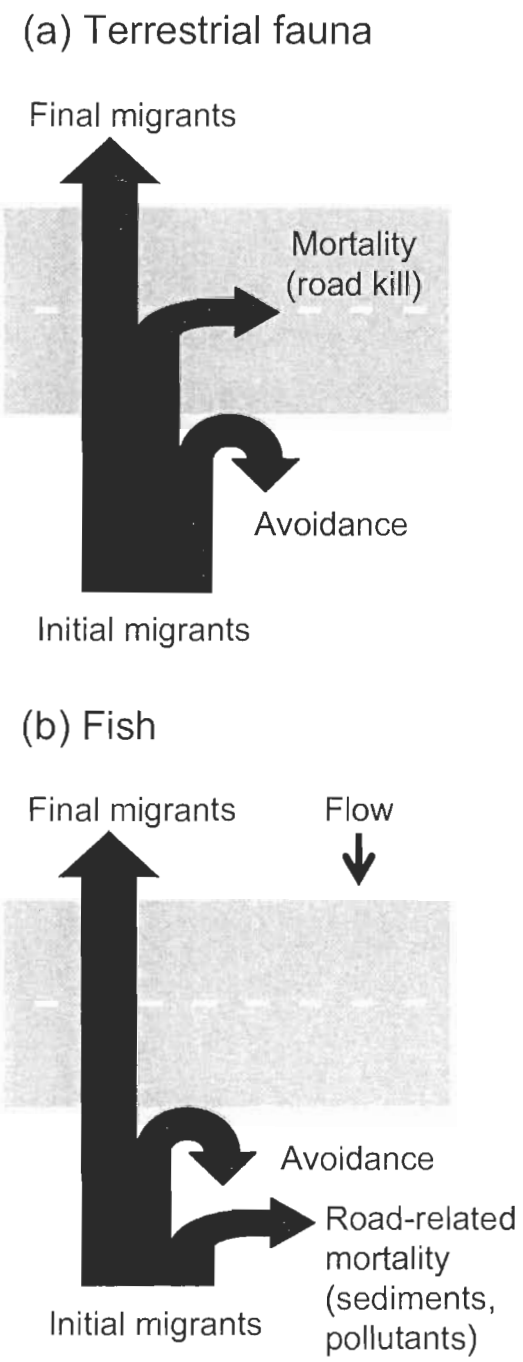
(a) Terrestrial fauna
Final migrants
Mortality
(road kill)
Avoidance
Initial migrants
(b) Fish
Final migrants
Flow
Avoidance
Road-related
mortality
(sediments,
pollutants)
Initial migrants

Figure S1

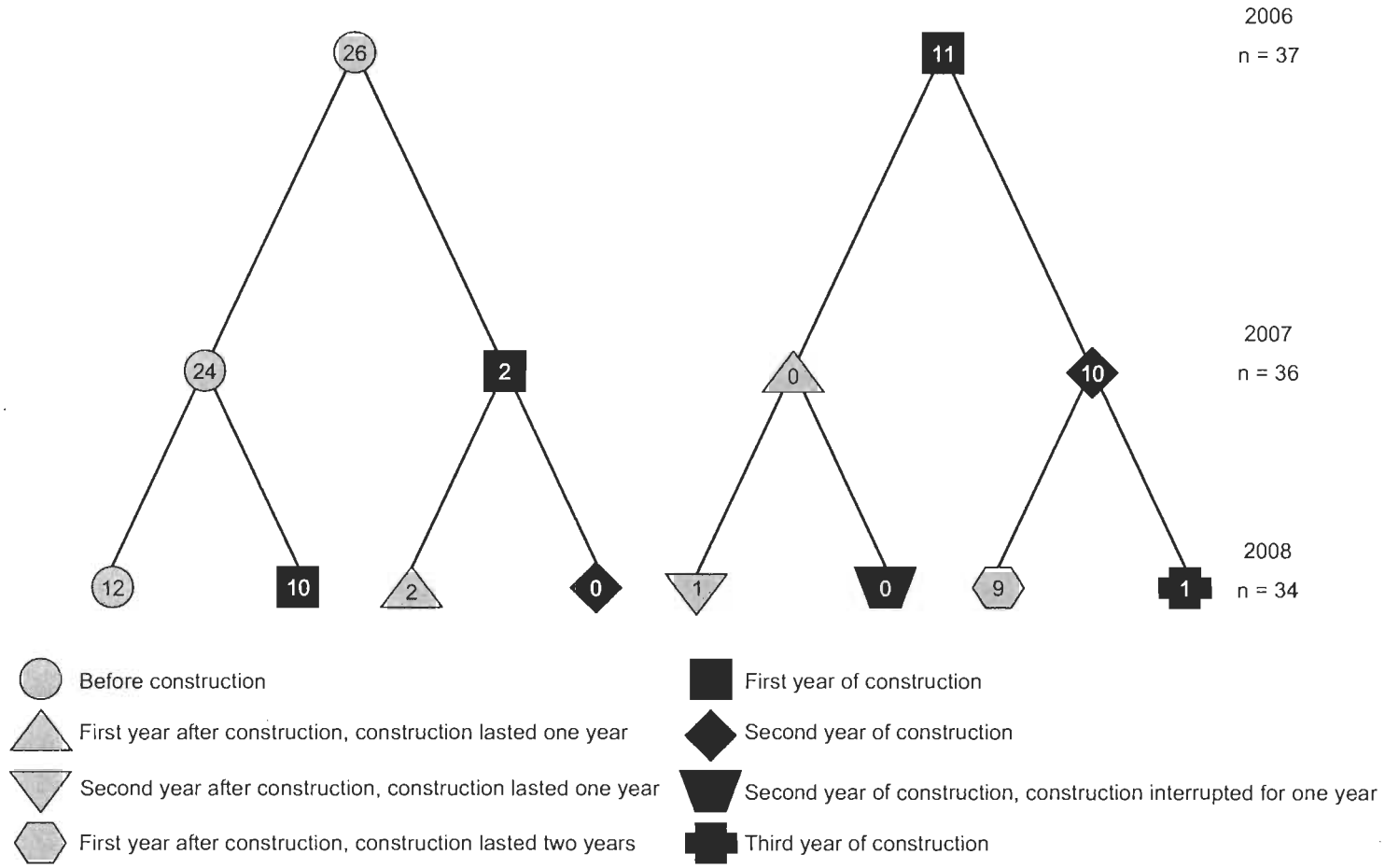
2006
n = 37
2007
n = 36
2008
n = 34
26
24
12
10
2
2
0
11
0
1
0
10
9
1
Before construction
First year after construction, construction lasted one year
Second year after construction, construction lasted one year
First year after construction, construction lasted two years
First year of construction
Second year of construction
Second year of construction, construction interrupted for one year
Third year of construction

Figure S2a

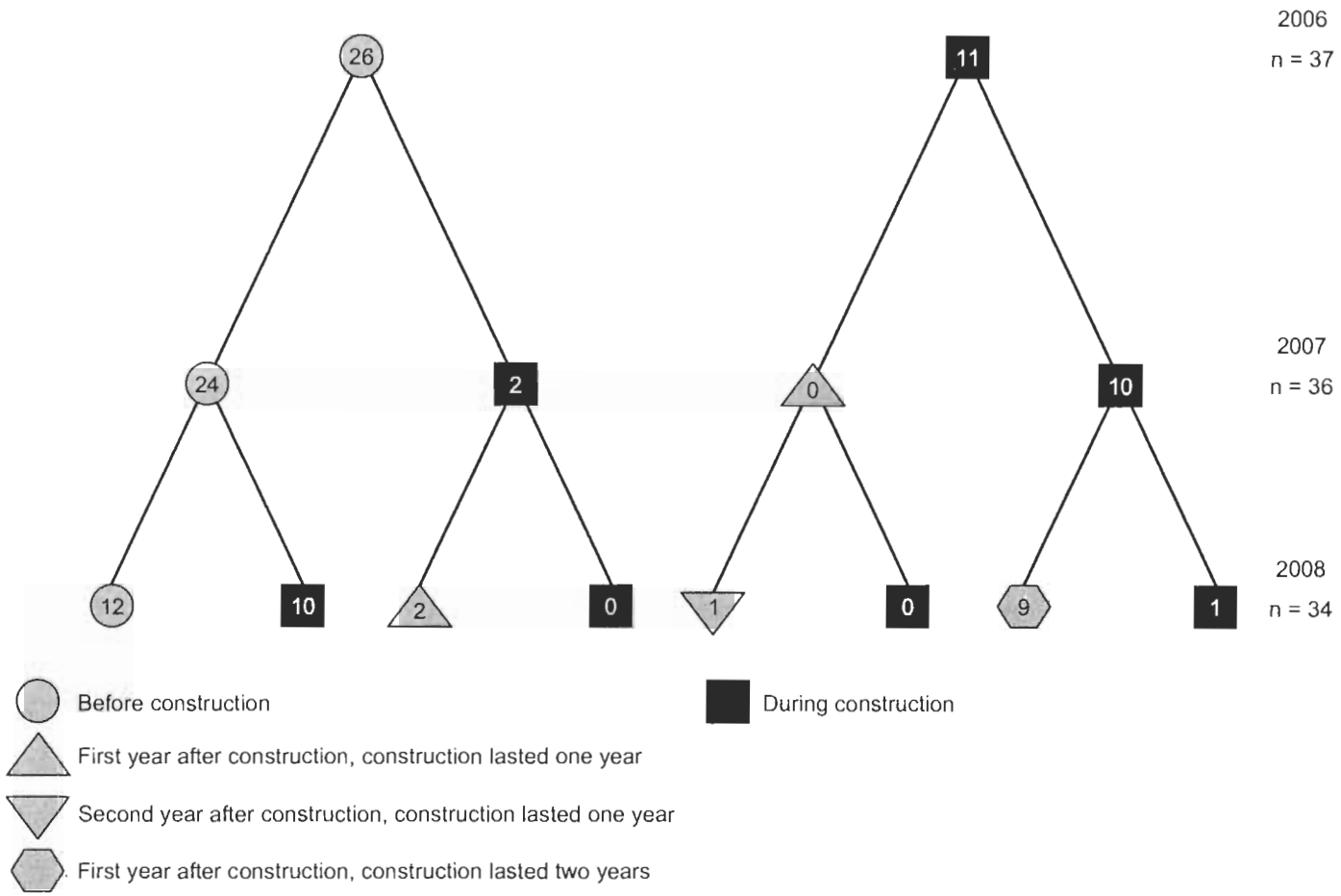
2006
n = 37
2007
n = 36
2008
n = 34
26
24
12
10
2
2
0
11
0
1
0
10
9
1
Before construction
During construction
First year after construction, construction lasted one year
Second year after construction, construction lasted one year
First year after construction, construction lasted two years

Figure S2b

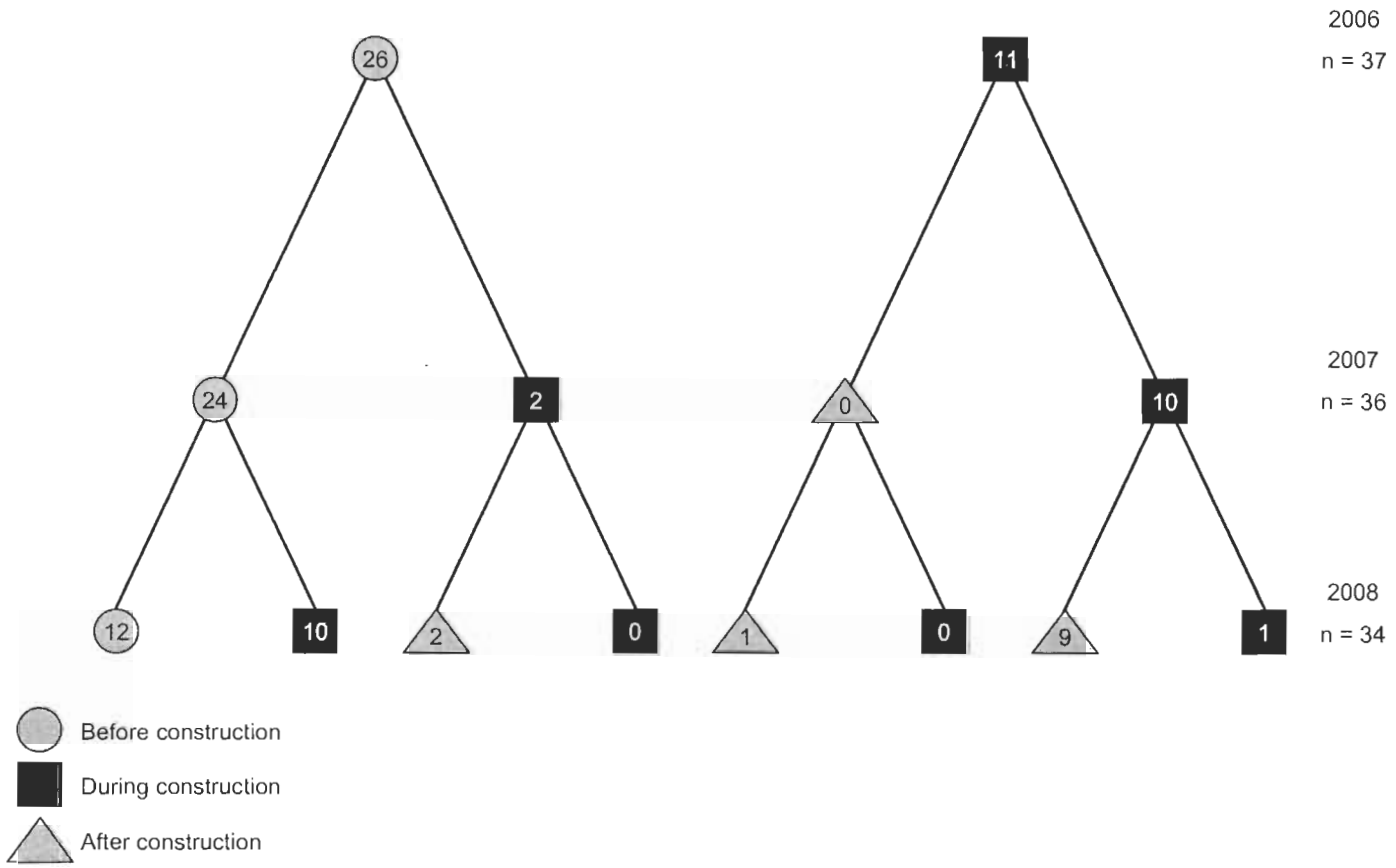
2006
n = 37
2007
n = 36
2008
n = 34
26
11
24
2
0
10
12
10
2
0
1
0
9
1
Before construction
During construction
After construction

Figure S2c

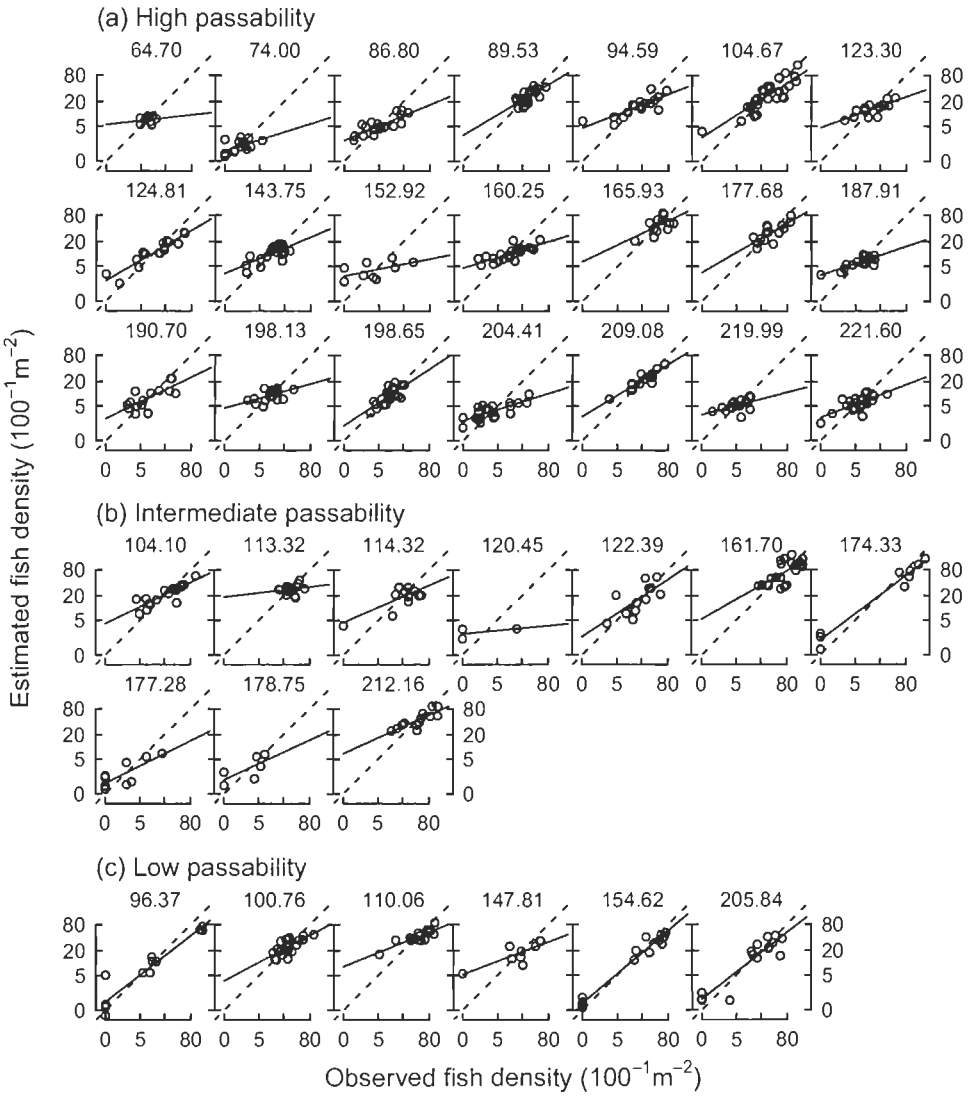
(a) High passability
64.70
74.00
86.80
89.53
94.59
104.67
123.30
124.81
143.75
152.92
160.25
165.93
177.68
187.91
190.70
198.13
198.65
204.41
209.08
219.99
221.60
(b) Intermediate passability
104.10
113.32
114.32
120.45
122.39
161.70
174.33
177.28
178.75
212.16
(c) Low passability
96.37
100.76
110.06
147.81
154.62
205.84
80
20
5
0
0 5 80
Estimated fish density (100^{-1}m^{-2})
Observed fish density (100^{-1}m^{-2})

Figure S3

Appendix S1. Specification of the Markovian random walk model

We represent fish movements by means of a discrete-time Markov chain with discrete state space $S = \{1, 2, \ldots, m - 1, m\}$. Movements are allowed only between adjacent states in a linear array that comprises an even number of segments, m, and has a barrier at its midpoint. To avoid edge effects, opposite edges of the array (representing states 1 and m) are connected to form a torus (Adler & Nuernberger 1994). Movements between segments (states) of the array are governed probabilistically by the m x m transition matrix **P**. The elements of **P**, p_{ij}, are transition probabilities that sum to unity across rows.

We assume that: 1) movement behaviors, including responses to a barrier, are density-independent, constant in time and identical across individuals; 2) population size and spatial distribution are at equilibrium; 3) fish follow a random walk that may be biased toward upstream or downstream movement; 4) potential barriers do not hinder downstream movement but may affect upstream movement of fish that encounter them. In the absence of barrier effects, fish move downstream with probability p_d, or upstream with probability $1 - p_d$. Fish encountering a barrier traverse it with probability k, or are unable to cross the barrier (are "reflected" by it) with probability $1 - k$. Parameter k quantifies the porosity, or passability, of the barrier and may thus vary across barrier types (see Rodríguez 2010 for a continuous-space version of this model). Based on these biological assumptions, the transition matrix **P** is constructed as follows:

$p_{i,i+1} = p_d$, for $i < m$

$p_{1,m} = 1 - p_d$

$p_{i,i-1} = 1 - p_d$, for $i \leq m/2$ or $i > m/2 + 1$

$p_{i,i-1} = k\,(1 - p_d)$, for $i = m/2 + 1$

$p_{i,i} = (1 - k)\,(1 - p_d)$, for $i = m/2 + 1$

$p_{m,1} = p_d$

$p_{i,i} = 0$, elsewhere.

The stationary distribution of the chain, $\boldsymbol{\pi}$ (the equilibrium distribution toward which the chain converges regardless of where it begins), has the following properties (Grimmett & Stirzaker 2001):

$\pi_j \geq 0$ for all j, and $\Sigma_j\, \pi_j = 1$

$\boldsymbol{\pi}\, \mathbf{P} = \boldsymbol{\pi}$, that is, $\pi_j = \Sigma_i\, \pi_i\, p_{ij}$, for all j.

Suppose that $\mathbf{I}_m$ is the identity matrix, $\mathbf{U}$ is an m x m matrix of ones, and $\mathbf{1}_m$ a row vector of ones. The stationary distribution $\boldsymbol{\pi}$ can be obtained by solving the equation:

$$\boldsymbol{\pi}\,(\mathbf{I}_m - \mathbf{P} + \mathbf{U}) = \mathbf{1}_m.$$

The stationary distribution for each barrier type (L: Low; I: Intermediate; H: High) can be expressed as a function of its constituent parameters: $\boldsymbol{\pi}_L(k_L, p_d)$, $\boldsymbol{\pi}_I(k_I, p_d)$, and $\boldsymbol{\pi}_H(k_H, p_d)$.

To fit the Markovian model to density estimates from the linear mixed model, we discretized the 1.6 km reach near the highway crossing (0.8 km to either side of the crossing; Fig. 4) into 100 16-m long segments and used the best-fitting linear mixed model (model 12; Table 1) to estimate density at the midpoint of each segment. Covariates year and stream width were set at their mean values. This procedure was performed separately for the three passability types, yielding density vectors $\boldsymbol{d}_{\mathrm{L}}$, $\boldsymbol{d}_{\mathrm{I}}$, and $\boldsymbol{d}_{\mathrm{H}}$. Least-squares estimates of parameters k_L, k_I, k_H, and p_d were obtained by minimizing the function:

$$\Sigma_m\{(\boldsymbol{d}_L - \boldsymbol{\pi}_L \Sigma_m \boldsymbol{d}_L/m)^2 + (\boldsymbol{d}_I - \boldsymbol{\pi}_I \Sigma_m \boldsymbol{d}_I/m)^2 + (\boldsymbol{d}_H - \boldsymbol{\pi}_H \Sigma_m \boldsymbol{d}_H/m)^2\},$$

where $m = 100$ and the $\Sigma_m \boldsymbol{d}/m$ term scales the stationary probabilities to densities.

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CHAPITRE II

FISH DISPERSAL IN FRAGMENTED LANDSCAPES: A MODELING FRAMEWORK FOR QUANTIFYING THE PERMEABILITY OF STRUCTURAL BARRIERS

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Résumé

La dispersion est un déterminant clé de la répartition spatiale et de l'abondance des populations, mais la fragmentation induite par l'homme peut créer des barrières qui entravent la dispersion et réduisent la viabilité des populations. Cette étude présente un cadre de modélisation basé sur des fonctions de dispersion (distributions de Laplace modifiées) qui décrit la dispersion des poissons en rivière en présence d'obstacles à leur libre circulation. Nous avons utilisé des expériences de marquage – recapture pour quantifier la dispersion estivale de l'omble de fontaine dans quatre cours d'eau traversés par une autoroute. L'analyse a identifié une hétérogénéité de la population dans le comportement de dispersion, comme révélé par la présence d'une composante sédentaire dominante (48 – 72 % de tous les individus) caractérisée par une dispersion moyenne courte (< 10 m), et une composante mobile secondaire caractérisée par une dispersion moyenne plus longue (56 – 1 086 m). Nous n'avons pas détecté d'évidence d'effets de barrière des traverses autoroutières sur la dispersion des poissons. La simulation de différents scénarios plausibles a indiqué que la détection des effets de barrière était fortement dépendante de caractéristiques du plan d'échantillonnage, tel que la configuration spatiale de la zone d'échantillonnage, l'étendue de la barrière, et la taille de l'échantillon. Le cadre de modélisation proposé étend les fonctions de dispersion conventionnelles en y incorporant les barrières structurales. La force majeure de l'approche est que le processus écologique (modèle de dispersion) et le plan d'échantillonnage (modèle d'observation) sont incorporés simultanément dans l'analyse. Cette caractéristique facilite l'utilisation des connaissances antérieures pour améliorer l'efficacité d'échantillonnage lors des expériences de marquage – recapture dans les études de mouvement. L'estimation du paramètre de perméabilité basée sur le modèle et son incertitude associée fournissent une approche rigoureuse pour quantifier l'effet des barrières sur la dispersion des poissons en rivière et pour évaluer les dynamiques de population des poissons en rivière dans des paysages fragmentés.

Mots-clés : barrières, connectivité, déplacement leptokurtique, écologie des routes, fonction de Laplace, marquage – recapture, mouvement, passage, plan d'échantillonnage, poisson de rivière, simulation, traverse autoroutière

Abstract

Dispersal is a key determinant of the spatial distribution and abundance of populations, but human-made fragmentation can create barriers that hinder dispersal and reduce population viability. This study presents a modeling framework based on dispersal kernels (modified Laplace distributions) that describe stream fish dispersal in the presence of obstacles to passage. We used mark-recapture trials to quantify summer dispersal of brook trout in four streams crossed by a highway. The analysis identified population heterogeneity in dispersal behavior, as revealed by the presence of a dominant sedentary component (48 – 72 % of all individuals) characterized by short mean dispersal (< 10 m), and a secondary mobile component characterized by longer mean dispersal (56 – 1086 m). We did not detect evidence of barrier effects on dispersal through highway crossings. Simulation of various plausible scenarios indicated that detectability of barrier effects was strongly dependent on features of sampling design, such as spatial configuration of the sampling area, barrier extent, and sample size. The proposed modeling framework extends conventional dispersal kernels by incorporating structural barriers. A major strength of the approach is that ecological process (dispersal model) and sampling design (observation model) are incorporated simultaneously into the analysis. This feature can facilitate the use of prior knowledge to improve sampling efficiency of mark-recapture trials in movement studies. Model-based estimation of barrier permeability and its associated uncertainty provides a rigorous approach for quantifying the effect of barriers on stream fish dispersal and assessing population dynamics of stream fish in fragmented landscapes.

Key-words: connectivity, highway crossings, barriers, leptokurtic displacement, Laplace kernels, mark-recapture, movement, passage, road ecology, sampling design, simulation, stream fish

Introduction

Dispersal, viewed in the most general sense as the way in which individuals move among sites, is a key process that influences population dynamics (Bowler and Benton 2005, Clobert et al. 2009), links metapopulations (Hanski 1998, Urban et al. 2009) and affects the spread of invasion (Kot et al. 1996, Clark et al. 2003). At the landscape scale, road networks are a growing source of human-made fragmentation (Forman and Alexander 1998, Riitters and Wickham 2003). Breaks in connectivity resulting from fragmentation can affect population dynamics and threaten many animal species (Fahrig and Merriam 1994, Letcher et al. 2007, Morita et al. 2009, Sanderson and Hubert 2009). In riverine landscapes, road construction often involves the installation of physical structures, such as culverts, that can restrict fish passage (Belford and Gould 1989, Warren and Pardew 1998, Burford et al. 2009). Restrictions to dispersal are often postulated to cause decline in genetic diversity and increase in extinction risk for populations in fragmented landscapes (Thomas 2000, Epps et al. 2005, Clark et al. 2010).

Numerous dispersal models have been developed to understand the dispersal of organisms in their natural landscape (Clark et al. 1999, Fujiwara et al. 2006, Lutscher 2007, Gurarie et al. 2009). Many studies integrate environmental factors into models for movement behavior (Okubo and Levin 2001), yet there is a paucity of models that explicitly incorporate discrete barriers to movement in fragmented landscapes (e.g., Schick et al. 2008, Rodríguez 2010). Here, we present a general modeling framework to analyze fish dispersal in fragmented riverine landscapes using mark-recapture data. This framework includes representations of both fish movements (ecological process) and data collection (sampling design) (Hilborn 1990, Clark 2007, Zurell et al. 2010). Our analyses are based on a movement model that explicitly quantifies the permeability of discrete barriers to dispersal (Rodríguez 2010). Additionally, we used

a simulation approach integrating both ecological process and sampling design to assess the detectability of barrier effects under various sampling scenarios.

Methods

Study site and sampling design

We investigated the impacts of highway crossings on brook trout (*Salvelinus fontinalis*) dispersal during the summers of 2007 and 2008. The study was carried out in the Laurentides Wildlife Reserve (47°45'N, 71°15'W), Quebec (Canada). Four streams crossed by highway 73/175, which runs between the cities of Quebec and Saguenay, were selected for study (Table 1). These streams were chosen because (1) habitat features (channel morphology, stream slope and width) were similar upstream and downstream of the highway, (2) no other potential obstacles to fish dispersal were apparent, and (3) brook trout were present at either side of the highway. The reinforced concrete structures present at the crossings were: rectangular portico with spillways and concrete substrate (two streams), rectangular portico with natural substrate, and open-bottom portico with natural substrate (Table 1; Appendix A). Natural substrate was coarse, with predominance of cobble and boulders. None of the crossing structures had outlet drops, and slopes at the four crossings were ≤ 2.42 % (Table 1), which suggests that these crossings were not major obstacles to brook trout passage (Poplar-Jeffers et al. 2009, Pépino et al. 2012).

In each of the four streams, we delimited two 240-m reaches, one downstream and the other upstream of the highway. Each reach comprised 12 adjacent 20-m sections (Fig. 1). Brook trout were collected by electrofishing (Smith-Root D-15) in an upstream direction starting at the section furthest downstream. Individual sections were closed at each extremity with seine nets (6-mm mesh) during the sessions of capture and recapture. Fish were free to disperse between the capture and recapture

sessions, during a period lasting four (2007) or five (2008) weeks (Table 1). One to three electrofishing passes were completed during the capture sessions. Sampling effort was kept constant at two passes during the recapture sessions.

Fish collected during the capture sessions were anesthetized (30 mg/L clove oil; Woody et al. 2002), measured (total length, TL, nearest mm), weighed (nearest g), and batch-marked with a section-specific code (combination of mark color and position). Marked fish were allowed to recover in a container for 10-15 min, and were then released near the center of the section where they were caught. Visible implant elastomer marks (Northwest Marine Technologies) were applied at two body locations, the adipose tissue behind the right or left eye and either between the fin rays of the right or left pectoral fin (individuals $\geq$ 50 mm TL) or at the base of the caudal fin (individuals < 50 mm TL). Four mark colors were used: blue, red, orange, and yellow. The combination of mark color and position allowed for unique identification of individual stream sections. At the time of recapture, all fish caught were measured, weighed and inspected in the shade under a lamp (NMT VI Light) designed to make the marks fluoresce, thus improving detectability (FitzGerald et al. 2004). Of a total of 1 343 fish marked, 374 were recaptured with two marks and 20 with one mark. The estimated mark retention rate, 97%, is comparable to than in previous studies using VIE marks (FitzGerald et al. 2004, Josephson et al. 2008). Brook trout density ranged from 11 to 50 fish 100^{-1} m^{-2} based on the first pass of electrofishing during the capture sessions. Brook trout used in the analyses (n = 374) were relatively small (*TL*: median = 72 mm; 1st quartile = 64 mm; 3rd quartile = 114 mm) and young (55.6% in the young-of-the-year age group).

Dispersal models

Empirical dispersal kernels are often leptokurtic (Kot et al. 1996, Fraser et al. 2001, Coombs and Rodríguez 2007, Petrovskii and Morozov 2009). The Laplace

(double exponential) kernel is a leptokurtic distribution that provides adequate fits to dispersal data in various salmonid species (Rodríguez 2002, Coombs and Rodríguez 2007).

The Laplace density function, f_L, depicts a symmetrical exponential decay to either side of the origin, with parameter δ that is equal to the mean dispersal distance in the population:

$$f_L(x,\delta) = \frac{1}{2\delta}\exp\left(\frac{-|x|}{\delta}\right)$$

where x is the distance from origin. In this formulation all individuals have a common dispersal behavior, characterized by parameter δ (i.e., the population is homogeneous). Extension of the Laplace kernel to fragmented landscapes is based on the assumption that fish confronting the barrier can either traverse the barrier or turn back (Rodríguez 2010). The model distinguishes among: (1) fish that do not reach the barrier; (2) fish that reach the barrier and are "reflected" and reverse their direction but do not otherwise alter their movement behavior (as measured by their displacement parameter); and (3) fish that traverse the barrier and do not alter their movement behavior (Rodríguez 2010). In this model, the permeability parameter, k, can be viewed as a population-level parameter corresponding to the proportion of fish actually crossing the barrier relative to that expected to cross if the barrier was completely passable (Fig. 2). In the context of a barrier to fish passage, k assumes a value of one when the barrier is completely passable and a value of zero when the barrier is impassable. The density function of the barrier Laplace kernel, f_{BL}, is defined as follows:

$$f_{BL}(x,\delta,k)=\begin{cases} f_L(x,\delta)+\exp\left(\dfrac{-|b|}{\delta}\right)(1-k)\,f_L(x-b,\delta), & \text{for } x\geq b \text{ and } b<0 \\ \exp\left(\dfrac{-|b|}{\delta}\right)k\,f_L(x-b,\delta), & \text{for } x<b \text{ and } b<0 \\ f_L(x,\delta)+\exp\left(\dfrac{-|b|}{\delta}\right)(1-k)\,f_L(x-b,\delta), & \text{for } x\leq b \text{ and } b>0 \\ \exp\left(\dfrac{-|b|}{\delta}\right)k\,f_L(x-b,\delta), & \text{for } x>b \text{ and } b>0 \end{cases}$$

where k is the permeability parameter, b is the distance between the barrier and the center of the section of capture (i.e., the distance from the barrier to the point of origin). The proportion of fish expected to cross the barrier in the absence of a barrier effect (k = 1), is given by the expression $\int_{|b|}^{\infty} f_L(x,\delta)=\frac{1}{2}\exp\left(\frac{-|b|}{\delta}\right)$ (gray area in Fig 2a). The Laplace kernel is retrieved from the barrier Laplace kernel by setting k = 1 (Rodríguez 2010).

Population heterogeneity in dispersal behavior is common in nature (Skalski and Gilliam 2000, Rodríguez 2002, Gurarie et al. 2009). The Laplace mixture accounts for population heterogeneity by combining two Laplace kernels, one for sedentary individuals and the other for mobile ones (Rodríguez 2002, Coombs and Rodríguez 2007). Extension of the barrier Laplace kernel to a heterogeneous population is straightforward (Rodríguez 2010). The density function of the barrier Laplace mixture kernel, f_{BLM}, combines two density functions of barrier Laplace kernel:

$$f_{BLM}(x,p,\delta_s,\delta_m,k)=p\,f_{BL}(x,\delta_s,k)+(1-p)\,f_{BL}(x,\delta_m,k)$$

where p is the proportion of sedentary individuals, δ_s is the mean dispersal for the sedentary individuals, and δ_m is the mean dispersal for the mobile individuals. The modeling framework presented here can be easily generalized to other types of dispersal kernels and extended to include multiple barrier effects occurring in highly fragmented landscapes (Appendix B). The models presented here assume that movement parameters are identical for upstream and downstream movements, implying symmetry and non-directionality of displacements. When these assumptions do not hold, asymmetric Laplace distributions (Kotz et al. 2001) or advection-diffusion models (Skalski and Gilliam 2000) may provide viable alternatives. Similarly, separate permeability values can be used for upstream and downstream movements whenever a barrier is not expected to be equally permeable in either direction.

We used the barrier Laplace and barrier Laplace mixture kernels to calculate movement probabilities for individual stream sections. We assigned to each fish a longitudinal distance between the center of the section where it was captured (or recaptured) and the center of the highway, and assigned positive and negative distance values for sections located downstream and upstream from the highway, respectively. These distances were used to calculate probabilities of movement between sections (dispersal matrix; below). If x_{j1} and x_{j2} are respectively the distances of the upstream and downstream boundaries of section j, then the probability, d_{ij}, that a fish from section i (distance x_i, which corresponds to the middle of section i) moves to section j, is given by the integral:

$$d_{ij}(\theta) = \int_{x_{j1}-x_i}^{x_{j2}-x_i} f(x,\theta)\, dx$$

where f is the density function of one of the two dispersal kernels described above (i.e, f_{BL} or f_{BLM}) and θ is the parameter set relative to this function. In this way, we

constructed a dispersal matrix, D, consisting in 24 rows (section of capture) and 24 columns (section of recapture) and filled by the d_{ij} values.

Observation models

Observation models incorporate the sampling design by describing how marked fish were recaptured and their tags reported (Hilborn 1990). The recapture data consist of counts for each of the 24 sections. We built a count matrix, Y, composed of 24 rows (section of capture) and 24 columns (section of recapture) where y_{ij} represents the number of fish marked in section i and recaptured in section j. The number of fish found in section j coming from section i (count matrix; above) is expected to be small. Thus, the observation models are based on a Poisson distribution, which gives in matrix notation:

$$Y \sim Pois(\mu)$$

where μ, the mean of the Poisson distribution, depends on the dispersal models and is estimated from the following equation:

$$\mu = N_0 \varphi_s \varphi_t \varphi_c D$$

where N_0 is the number of fish marked in the section of capture, D is the dispersal matrix, φ_s is the probability of survival during the study period, φ_t is the probability of retaining the two marks, and φ_c is the probability of capture for two consecutive passes. These last three terms are confounded and can be summarized into a single parameter, φ (hereafter probability of recapture). By simplifying and readjusting the last two equations, we obtain:

$$Y \sim Pois(N_0 \varphi D)$$

This equation incorporates both ecological process (dispersal model) and sampling design (observation model). The Poisson probability function, g, can be rewritten as:

$$g(y_{ij}, n_{0i}, \theta, \varphi) = \frac{\exp(-n_{0i}\varphi d_{ij}(\theta)) \cdot (n_{0i}\varphi d_{ij}(\theta))^{y_{ij}}}{y_{ij}!}$$

where y_{ij} and n_{0i} are data and θ and φ are parameters to be estimated (see *Model fitting and comparison*). This general modeling framework has broad applicability in mark-recapture studies of fish movement in streams and rivers.

Simulation approach

The two main objectives of the simulations were to (1) determine whether barrier effects were detectable with the available data (*Scenario 1*) and (2) identify constraints influencing the detectability of barrier effects in similar mark-recapture trials (*Scenario 2*). We followed the general simulation procedure proposed by Skarpaas et al. (2005):

1. Simulate fish dispersal based on a barrier Laplace mixture kernel (dispersal model);
2. Sample fish from individual sections (observation model);
3. Fit a barrier Laplace mixture model to the simulated data (estimation step);
4. Compare estimated permeability parameters to predetermined permeability parameters used to generate the simulated data;
5. Repeat steps 1 – 4 a number of times (100 iterations, unless otherwise specified).

In step 1, we used the observed longitudinal distribution of marked fish as initial conditions (Appendix C).

Scenario 1 – The barrier Laplace mixture models were simulated using the parameters estimated from our field data set for five different values of k (0.2, 0.4, 0.6, 0.8, and 1.0). We computed 1 100 iterations per value of k and compared the results of the 100 first iterations against the results of the 1 000 last iterations (Samietz and Berger 1997, Skarpaas et al 2005, Bolker 2008). Results were similar for the two sets of iterations; we therefore used 100 iterations in Scenario 2 to reduce computation time (see *Results*).

Scenario 2 – The detectability of barrier effects can depend on both design and ecological constraints. In scenario 2, we examined potential ecological (dispersal distance for mobile individuals, δ_m, and strength of barrier effect, k) and design (the number of individuals susceptible to recapture, φN_0, and highway width) constraints (Table 2). Highway width is a potential constraint on detectability because as highway width increases the study reaches become more distant from the center of the highway, which reduces the probability of recapturing marked fish that have encountered the barrier (gray area in Fig. 2), i.e., those that convey information on barrier effects.

The relative contribution of ecological and design constraints to detectability of barrier effects was analyzed under various parameter combinations. We fixed the dispersal parameters to match both the range of values found in our study and those reported previously for brook trout (Rodríguez 2002). Specifically, we simulated barrier Laplace mixture models (p = 0.7; δ_s = 10 m) for three values of δ_m (60, 300, and 1500 m) and five values of k (0.2, 0.4, 0.6, 0.8, and 1.0). We fixed φ at 0.4, a value similar to those found in our study (see *Results*). Each combination of parameters is repeated for three levels of sample size (φN_0, $2\varphi N_0$, and $4\varphi N_0$) and two highway widths (actual and 20 m), resulting in a total of 36 000 simulations (Table 2). Upstream and downstream stream reaches in the simulations were identical to those in the field study (12 adjacent 20-m sections).

Model fitting and comparison

Parameter estimates for all models were obtained through numerical minimization of the negative logarithm of the likelihood function, L:

$$L(y_{ij}, n_{0i}, \theta, \varphi) = \prod_{j=1}^{S} \prod_{i=1}^{S} g(y_{ij}, n_{0i}, \theta, \varphi)$$

where S is the number of stream sections (S = 24). Model selection was based on Akaike's Information Criterion adjusted for small sample sizes, AIC_c (Burnham and Anderson 2002). Dispersal models were ranked according to ΔAIC_c, the difference between the AIC_c of a candidate model and that of the model with the lowest AIC_c (Burnham and Anderson 2002). The detectability of barrier effect was based on the 95% confidence interval of k: when the 95% confidence interval of k did not include 1, we considered that a barrier effect was detected. All calculations were done in the R environment (R development Core Team 2010).

Results

The barrier Laplace mixture model was better supported by the field data than the barrier Laplace model; this result was consistent for the four streams studied (Table 3). Parameter estimates for this model were also consistent among streams, with the exception of stream 124.81, where the proportion of sedentary individuals was smaller and the mean dispersal for mobile individuals greater than for the three other streams (Fig. 3, Table 4). The proportion of sedentary individuals ranged from 0.48 to 0.72. Sedentary individuals had mean dispersal < 10 m. In contrast, the mean dispersal for mobile individuals ranged from 56 to 1 086 m, and was estimated less precisely, as shown by the 95 % confidence intervals (Table 4). The median dispersal for brook trout populations was < 400 m in the stream 124.81 and < 55 m in the three

other streams. A total of 18 fish (4.8 % of all fish recaptured) crossed the highway during the study period; there was no apparent directionality in crossing direction (Fig. 4, Table 5). Values of k were not distinguishable from one (i.e., no barrier effect) for any of the streams. Estimates of k for streams 165.93 and 209.08 were uninformative, as shown by their 95 % confidence intervals (Table 4).

Scenario 1

Simulations showed that barrier effects were hardly detectable under scenarios corresponding to our field design even at very low barrier permeabilities (Appendix D). The number of crossings expected in the absence of barrier effect ($k = 1$) was very similar to the observed number of crossings (Table 5). Both the observed and expected number of crossings in the absence of a barrier effect were very small, indicating that the potential to detect any reductions in passage from this baseline is severely limited under the conditions simulated in scenario 1 (Table 5; Appendix D).

Scenario 2

Estimates of permeability (k) in simulation runs showed little evidence of bias, but precision was often very low for estimates near the upper and lower boundaries for k, especially under conditions matching those in our field study (sample size = φN_0; actual highway width) (Appendix E). Precision of estimates of k was markedly greater for 20-m highway width than for actual highway width and also increased with increases in sample size (Appendix E). The mean dispersal for mobile individuals also affected precision, which was greater for $\delta_m = 300$ m than for $\delta_m = 60$ m or $\delta_m = 1500$ m (Appendix E).

Differences in precision led to differences in power to detect barrier effects. Unsurprisingly, power to detect a barrier effect increased systematically with effect

size and sample size (Fig. 5). Power was greatest for δ_m = 300 m and 20-m highway width; however, even under this favorable combination, power to detect a 20% reduction in barrier passability (k = 0.8) was lower than 38% (Fig. 5). Power was uniformly low when highway width matched that used in the field study and mobile individuals had low dispersal (δ_m = 60 m), but increased markedly in simulated increase in mobility (δ_m = 300 and 1500 m) or simulated decline in highway width (to 20 m) (Fig. 5).

In our study design, the only information available on barrier permeability is provided by fish that confront the barrier and either traverse it or are reflected by it. The expected number of marked fish that encounter the barrier and are subsequently recaptured ($N_{barrier}$; gray area in Fig. 2) depended on both ecological (dispersal parameter for mobile individuals) and design (sample size and highway width) features (Fig. 6A). Power to detect an existing barrier effect was strongly dependent on $N_{barrier}$ (Fig. 6B). These results provide further context for interpreting the lack of power observed under scenario 1, in which values of $N_{barrier}$ never exceeded 12 (Fig. 6A, Table 5).

Discussion

The main contributions of our modeling framework are that it can 1) efficiently use data from mark-recapture field trials to quantify the permeability of potential barriers to fish dispersal; 2) assess, via simulation, the statistical power of candidate sampling designs; 3) help identify changes in sampling design that could lead to increased power with little or no additional cost. We found no evidence of barrier effects on fish dispersal through highway crossings in the study streams, which was supported by the estimates of the permeability parameter and the number of crossings. However, simulation analyses showed that power to detect a barrier effect was low in most cases under conditions encountered in our field study. This lack of

power seems to be a consequence of the limited mobility of brook trout populations during the summer period. Although the median dispersal for brook trout populations were within the range of dispersal distances previously reported for brook trout (Riley et al. 1992, Rodríguez 2002, Peterson and Fausch 2003), dispersal was limited relative to the length of the study reaches and the width of the highway crossings (Fig.1, Tables 1 and 4). Power to detect an existing barrier effect was strongly dependent on $N_{barrier}$ (the expected number of marked fish that encounter the barrier and are subsequently recaptured), and $N_{barrier}$ in turn depends on fish mobility and distance from section of origin to the barrier (stationary individuals far from a barrier will likely never confront it). Simulations also showed that power would be improved substantially in settings having narrower highway crossings (20-m width) or greater sample sizes (two- or four-fold increase) than those in our field study. Summer does not appear to be a critical period for dispersal in brook trout; however, dispersal in brook trout and other salmonids can be episodic, with movement rates greatest in spring and autumn (e.g., Gowan and Fausch 1996). Studies that specifically aim to identify critical seasonal windows for dispersal in mobile stream fishes should be conducted over periods during which ecologically relevant dispersal (e.g., spawning movements) is likely.

Efficient sampling designs are required to obtain precise and accurate estimates of dispersal parameters in mark-recapture studies (Samietz and Berger 1997, Skarpaas et al. 2005, Cooper et al. 2008, Horton and Letcher 2008). Statistical power was strongly dependent on $N_{barrier}$, which suggests that maximizing $N_{barrier}$ subject to cost constraints is a valuable heuristic approach for improving sampling design. It is possible to compare estimates of $N_{barrier}$ obtained analytically (by integrating to obtain the gray area under the kernel in Fig. 2) under different plausible sampling scenarios. The finding that power values were greatest at intermediate values of mean dispersal distance (Figs. 5 and 6) suggests that, for a given mean dispersal distance, $N_{barrier}$ can be optimized by judicious placement of the boundaries of the study reaches. Although

the use of constant section lengths conveniently simplifies calculations, study sections of irregular length can be readily accommodated within the proposed framework. Prior knowledge about dispersal distances of target species can be used in this analysis, or, when such knowledge is unavailable, dispersal distances can be included among the constraints considered in the sampling scenarios (Dewhirst and Lutscher 2009). In studies comparing species of differing mobility and swimming capacity, design features affecting $N_{barrier}$, such as the length and positioning of study reaches, can be evaluated by simulation to assess statistical power for all species at different levels of barrier permeability.

Dispersal is often viewed as a critical determinant of the spatial distribution and abundance of populations (Bahn et al. 2008, Dewhirst and Lutscher 2009, Foldvik et al. 2010). Understanding how dispersal is affected in fragmented landscapes can clarify issues concerning population persistence, for example, whether high dispersal renders species more vulnerable (Funk et al. 2005) or less vulnerable (Thomas 2000) to fragmentation. Our modeling framework incorporates both ecological process and sampling design to provide unbiased estimates of dispersal and barrier permeability from mark-recapture data. Dispersal models incorporating barrier permeability can be incorporated in graph theory (Urban et al. 2009, Lookingbill et al. 2010) or population viability analyses (Lindenmayer et al. 2003) to achieve a better understanding of population dynamics in fragmented landscapes. The permeability parameter provides a quantitative estimate of barrier effect that can be used to assess the efficacy of structures designed to facilitate fish passage at crossings. To this end, field studies can be conducted to link features of crossing structures commonly considered in management policies (Ead et al. 2002, Larinier 2002, Meixler et al. 2009, Poplar-Jeffers et al. 2009) to barrier permeability as measured by parameter k.

Standard mark-recapture studies do not explicitly quantify the effect of barriers on the dispersal kernel. An important limitation of such studies in determining the

effects of potential barriers, particularly if they are partial barriers, on fish movements is that they only yield an overall rate of movement across the barrier, without indicating the extent to which that rate is restricted by the barrier. A key message to managers is that mark-recapture studies can be made more effective by: (1) modeling barrier effects on the dispersal kernel to quantify movement rates and barrier permeability with associated measures of uncertainty, (2) covering critical periods for dispersal, and (3) attaining sample sizes needed to satisfy power requirements.

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Table 1. Summary of mark-recapture trials and type of reinforced concrete crossing structure, by stream. Type: (a) rectangular portico with spillways and concrete substrate, (b) rectangular portico with natural substrate, and (c) open-bottom portico with natural substrate. Highway width is the distance between the upstream and downstream sampling reaches. Numbers of marked (n_0) and recaptured (n_f) fish and dates of capture (t_0) and recapture (t_f) are presented. Streams are identified by milepost distance

Stream (milepost distance)	Type	Height (m)	Width (m)	Length (m)	Slope (%)	Number of spillways	Highway width (m)	n_0	n_f	t_0	t_f
124.81	a	2.10	2.40	87	0.70	9	130	757	158	24/06/08 – 01/07/08	04/08/08 – 08/08/08
165.93	b	1.69	3.50	44	0.92	0	50	136	39	17/06/08 – 20/06/08	28/07/08 – 31/07/08
187.91	c	2.30	6.10	65	1.65	0	100	190	58	03/07/07 – 05/07/07	07/08/07 – 14/08/07
209.08	a	1.75	3.66	112	2.42	24	130	260	119	09/07/07 – 11/07/07	14/08/07 – 16/08/07

Table 2. Parameter settings used in simulations quantifying power to detect a barrier effect. The proportion of stationary individuals ($p = 0.7$), mean dispersal of stationary individuals ($\delta_s = 10$ m) and probability of recapture ($\varphi = 0.4$) were held constant for all simulations. A set of 100 simulations was run under each possible parameter combination ($n = 90$), for each of the four study streams (36 000 simulation runs in all). N_0: number of marked fish

Design constraints		Ecological constraints	
Highway width	Sample size	Mean dispersal for mobile individuals	Barrier permeability
Actual	$1\ \varphi\ N_0$	$\delta_m = 60$ m	$k = 0.2$
20 m	$2\ \varphi\ N_0$	$\delta_m = 300$ m	$k = 0.4$
	$4\ \varphi\ N_0$	$\delta_m = 1500$ m	$k = 0.6$
			$k = 0.8$
			$k = 1.0$

Table 3. Comparison of candidate models based the adjusted Akaike Information Criterion (AIC_c). Number of model parameters (Q) and difference in AIC_c relative to the best-fitting model (ΔAIC_c) are presented. Streams are identified by milepost distance

Stream (milepost distance)	Model					
	Barrier Laplace			Barrier Laplace mixture		
	Q	AIC_c	ΔAIC_c	Q	AIC_c	ΔAIC_c
124.81	3	291.0	184.9	5	106.1	0.0
165.93	3	163.4	18.7	5	144.7	0.0
187.91	3	227.9	55.8	5	172.1	0.0
209.08	3	176.5	42.1	5	134.4	0.0

Table 4. Parameter estimates for the barrier Laplace mixture models (95% confidence intervals given in parentheses). Streams are identified by milepost distance. p: proportion of sedentary individuals; δ_s: mean dispersal for sedentary individuals (m); δ_m: mean dispersal for mobile individuals (m); k: barrier permeability; φ: probability of recapture

Parameter	Stream (milepost distance)			
	124.81	165.93	187.91	209.08
p	0.48 (0.03 – 0.97)	0.72 (0.43 – 0.90)	0.72 (0.47 – 0.88)	0.68 (0.49 – 0.82)
δ_s (m)	8 (7 – 11)	6 (3 – 13)	7 (4 – 11)	6 (4 – 9)
δ_m (m)	1 086 (14 – 82 123)	74 (28 – 199)	259 (35 – 1 896)	56 (29 – 105)
k	1.02 (0.44 – 1.58)	1.98 (0.00- 2.00)	1.02 (0.19 – 1.83)	1.96 (0.00 – 2.00)
φ	0.37 (0.03 – 0.91)	0.31 (0.22 – 0.42)	0.36 (0.24 – 0.50)	0.50 (0.41 – 0.59)

Table 5. Observed and expected number of fish crossing the highway over the study period. Upstream and downstream refer to the reaches in which the fish were recaptured. The expected number of crossings was calculated using parameter estimates for the barrier Laplace mixture model (see Table 4), assuming that the barrier had no effect ($k = 1$). Streams are identified by milepost distance. n_f: number of recaptured fish

Stream (milepost distance)	n_f	Number of crossings			
		Upstream	Downstream	Observed	Expected
124.81	158	3	9	12	12
165.93	39	0	2	2	1
187.91	58	3	0	3	3
209.08	119	1	0	1	0
Total	**374**	**7**	**11**	**18**	**16**

Figure legends

Figure 1. Schematic representation of the mark-recapture sampling design. Vertical marks delimit the 20-m sections. Gray rectangles represent areas not sampled.

Figure 2. Dispersal kernels in fragmented riverine landscapes. Vertical broken lines represent the center of the highway. (a) The barrier Laplace kernel is continuous in absence of a barrier effect ($\delta = 100$ m; $k = 1$). (b) The barrier Laplace kernel is discontinuous in the presence of a barrier effect ($\delta = 100$ m; $k = 0.6$). Gray area: fish that would cross the highway in the absence of barrier effect (a) are redistributed to either side of the highway (b) as determined by the permeability parameter k.

Figure 3. (a) Fitted barrier Laplace mixture kernels (parameter values given in Table 4). The vertical broken line represents a hypothetical barrier placed 30 m downstream from the origin. (b) Close-up near the barrier. Streams are identified by milepost distance.

Figure 4. Observed dispersal during the study period. Solid circles represent fish that crossed the highway. The 1:1 line (solid lines) and center of the highway (broken lines) are shown. Position relative to the highway is represented by negative (upstream) and positive (downstream) distances. Streams are identified by milepost distance.

Figure 5. Power to detect a barrier effect (% of simulations in which the 95% confidence interval for k did not include 1). Simulations from barrier Laplace mixture models ($p = 0.7$; $\delta_s = 10$ m) are shown for three values of δ_m (60, 300, or 1500 m) and five values of k (0.2, 0.4, 0.6, 0.8, or 1.0). φ was fixed at 0.4. Symbol shapes represent three levels of sample size (circles: φN_0; squares: $2\varphi N_0$; triangles: $4\varphi N_0$). Black and

gray symbols represent actual and 20-m highway widths, respectively. Streams (horizontal rows) are identified by milepost distance.

Figure 6. Expected number of marked fish that encounter the barrier and are subsequently recaptured ($N_{barrier}$). Panel A: $N_{barrier}$ depends on the dispersal parameter for mobile individuals (x-axis), the sample size (symbol shape) and the highway width (symbol color). Circles: φN_0; squares: $2\varphi N_0$; triangles: $4\varphi N_0$. Black and gray symbols refer to actual and 20-m highway widths, respectively. Parameter values are set as follows: $p = 0.7$; $\delta_s = 10$ m; $k = 1$; $\varphi = 0.4$. $N_{barrier}$ is equivalent to the number of crossings when $k = 1$. Panel B: Power to detect a barrier effect as a function of $N_{barrier}$ and k. Circle size is proportional to the detectability of barrier effects (%). Streams are identified by milepost distance.

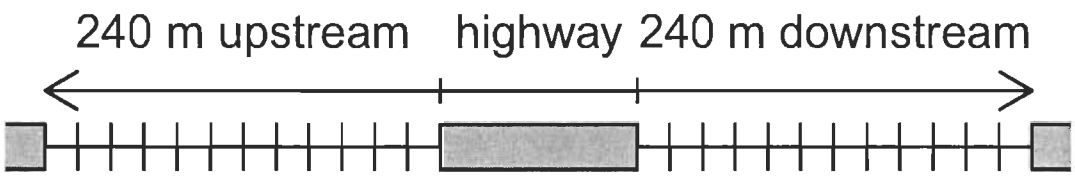

Figure 1

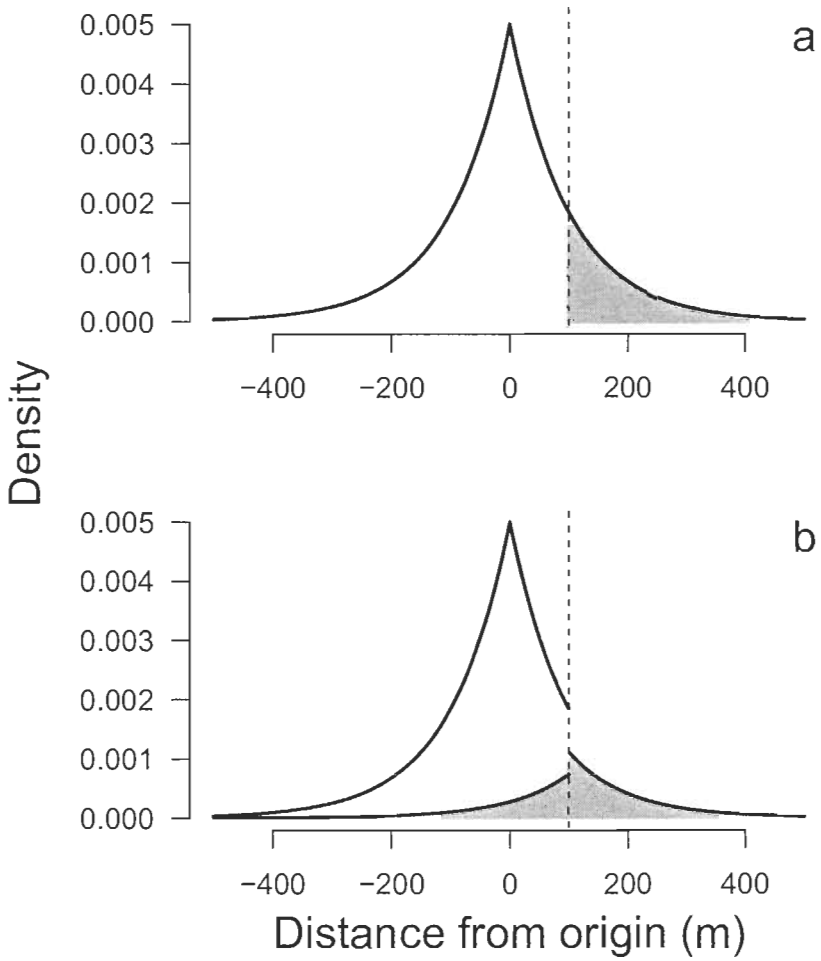
a
b
0.005
0.004
0.003
0.002
0.001
0.000
−400
−200
0
200
400
Density
Distance from origin (m)

Figure 2

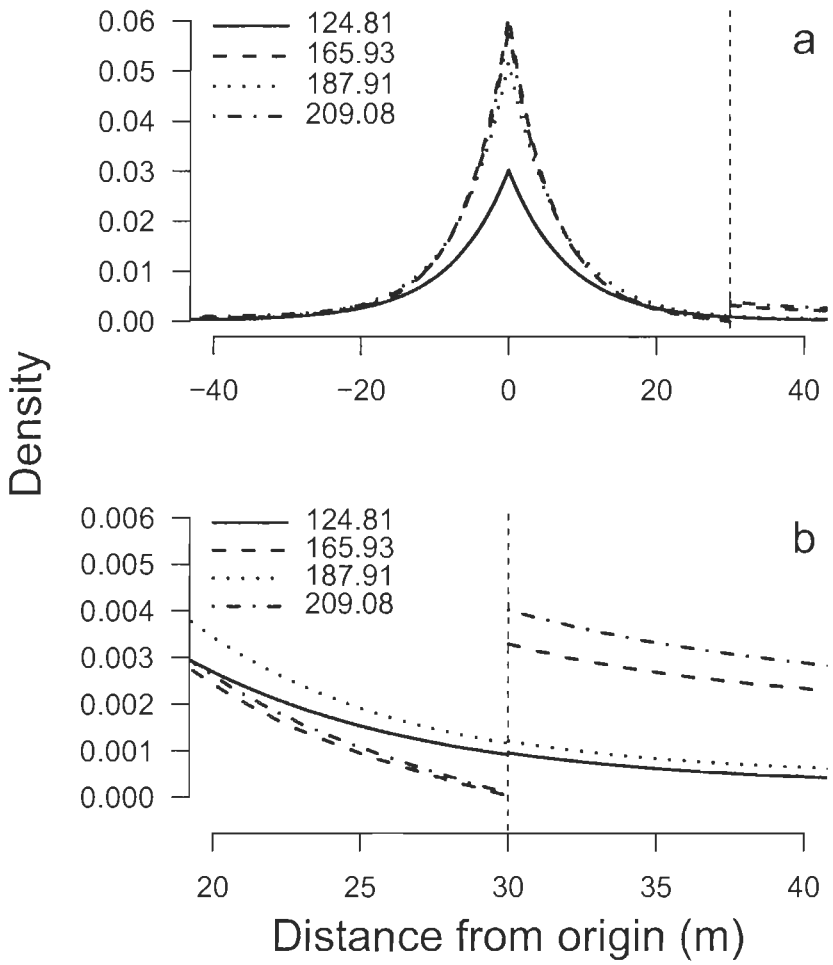
0.06
0.05
0.04
0.03
0.02
0.01
0.00
124.81
165.93
187.91
209.08
a
−40
−20
0
20
40
Density
0.006
0.005
0.004
0.003
0.002
0.001
0.000
124.81
165.93
187.91
209.08
b
20
25
30
35
40
Distance from origin (m)

Figure 3

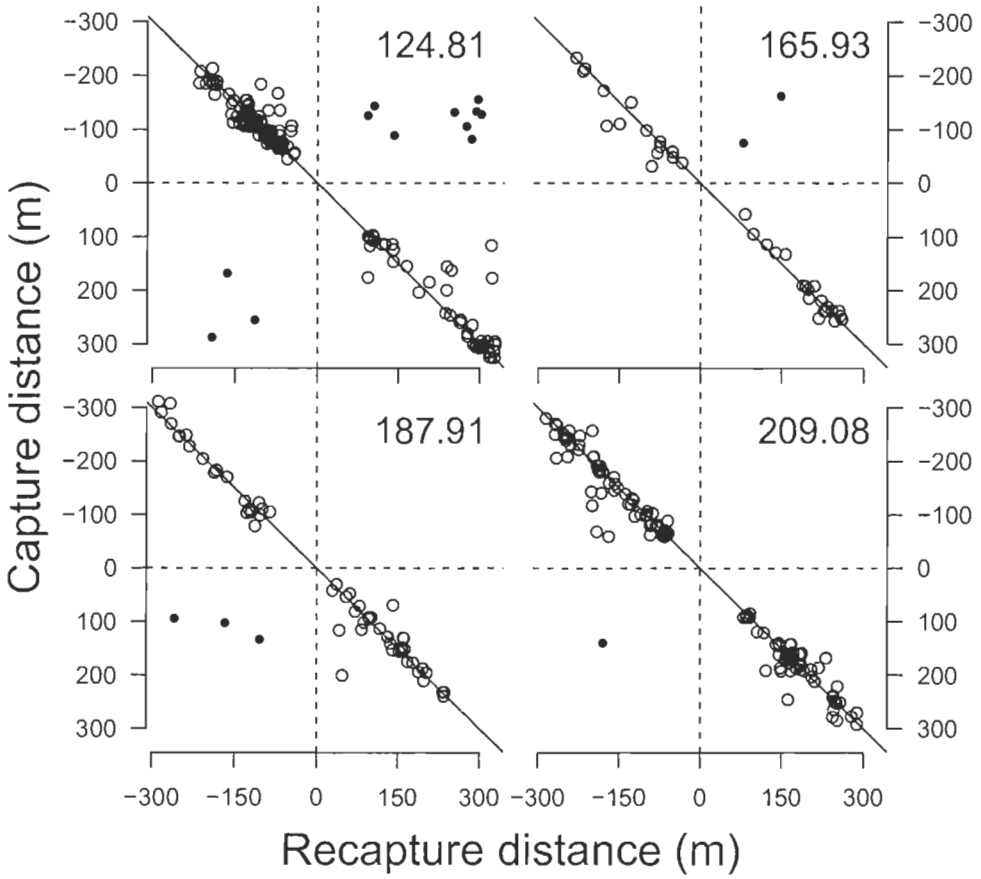
124.81
165.93
187.91
209.08
Capture distance (m)
Recapture distance (m)
−300
−200
−100
0
100
200
300
−150
150

Figure 4

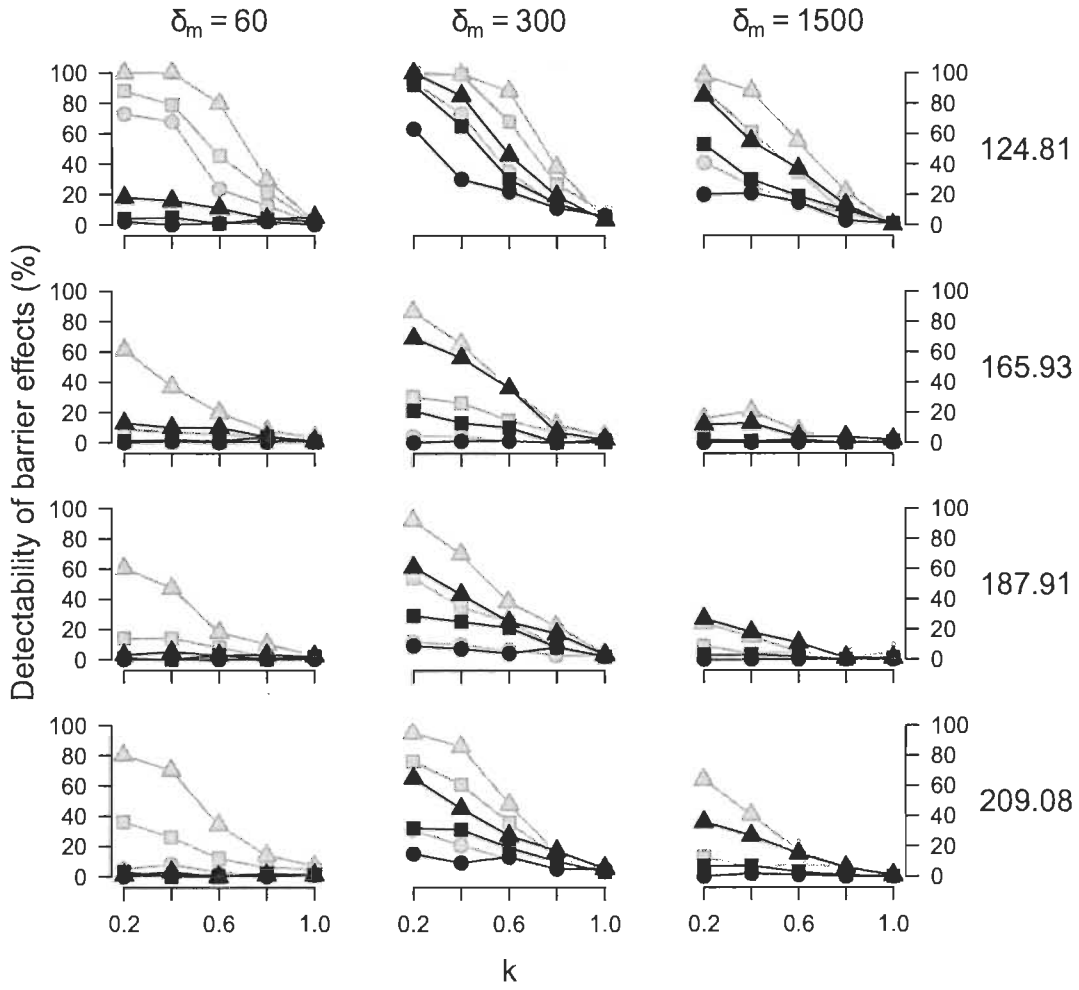
δm = 60
δm = 300
δm = 1500
Detectability of barrier effects (%)
124.81
165.93
187.91
209.08
k
0.2
0.6
1.0
0
20
40
60
80
100

Figure 5

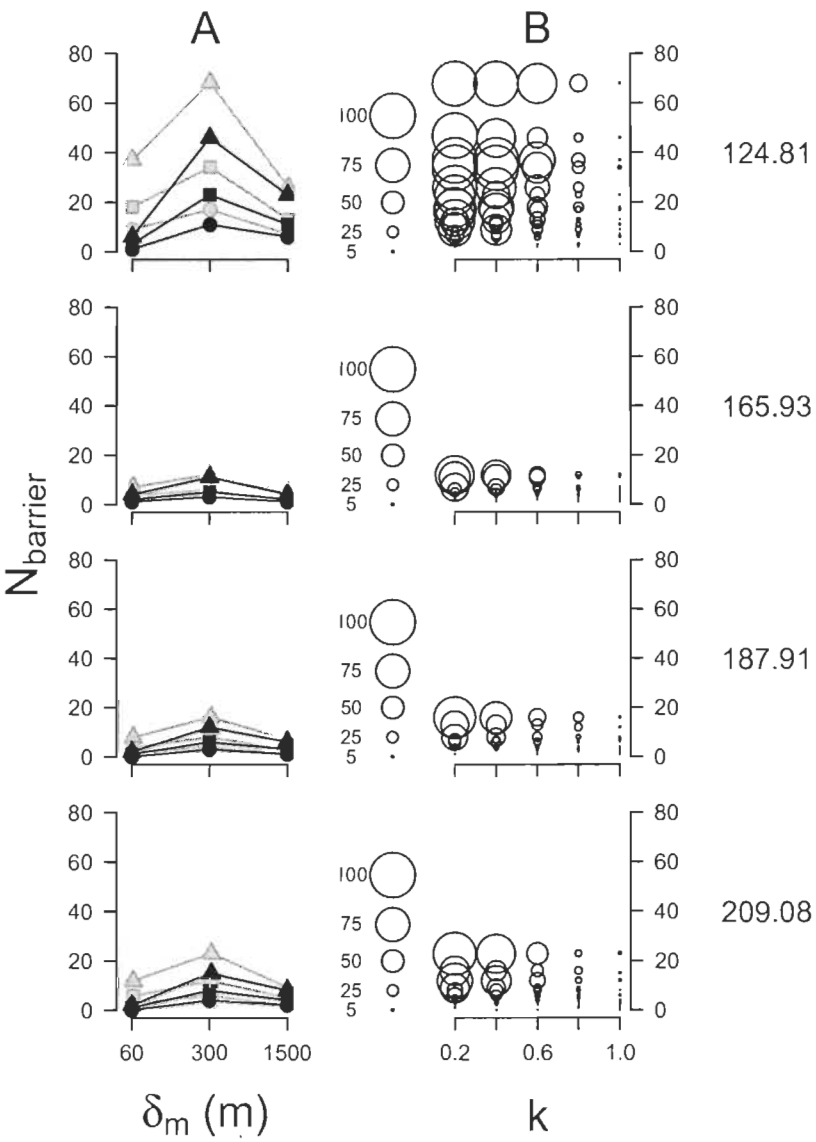
A
B
$N_{barrier}$
124.81
165.93
187.91
209.08
δ_m (m)
k
60
300
1500
0.2
0.6
1.0

Figure 6

Appendix A

Highway crossing structures at the four study streams. Rectangular portico with spillways and concrete substrate (a: stream 124.81; b: stream 209.08); rectangular portico with natural substrate (c: stream 165.93); open-bottom portico with natural substrate (d: stream 187.91). Spillway at the upstream end of the portico (e: stream 124.81). Streams are identified by milepost distance. Photo credits: Marc Pépino (a, b, d, e) and Yves Paradis (c).

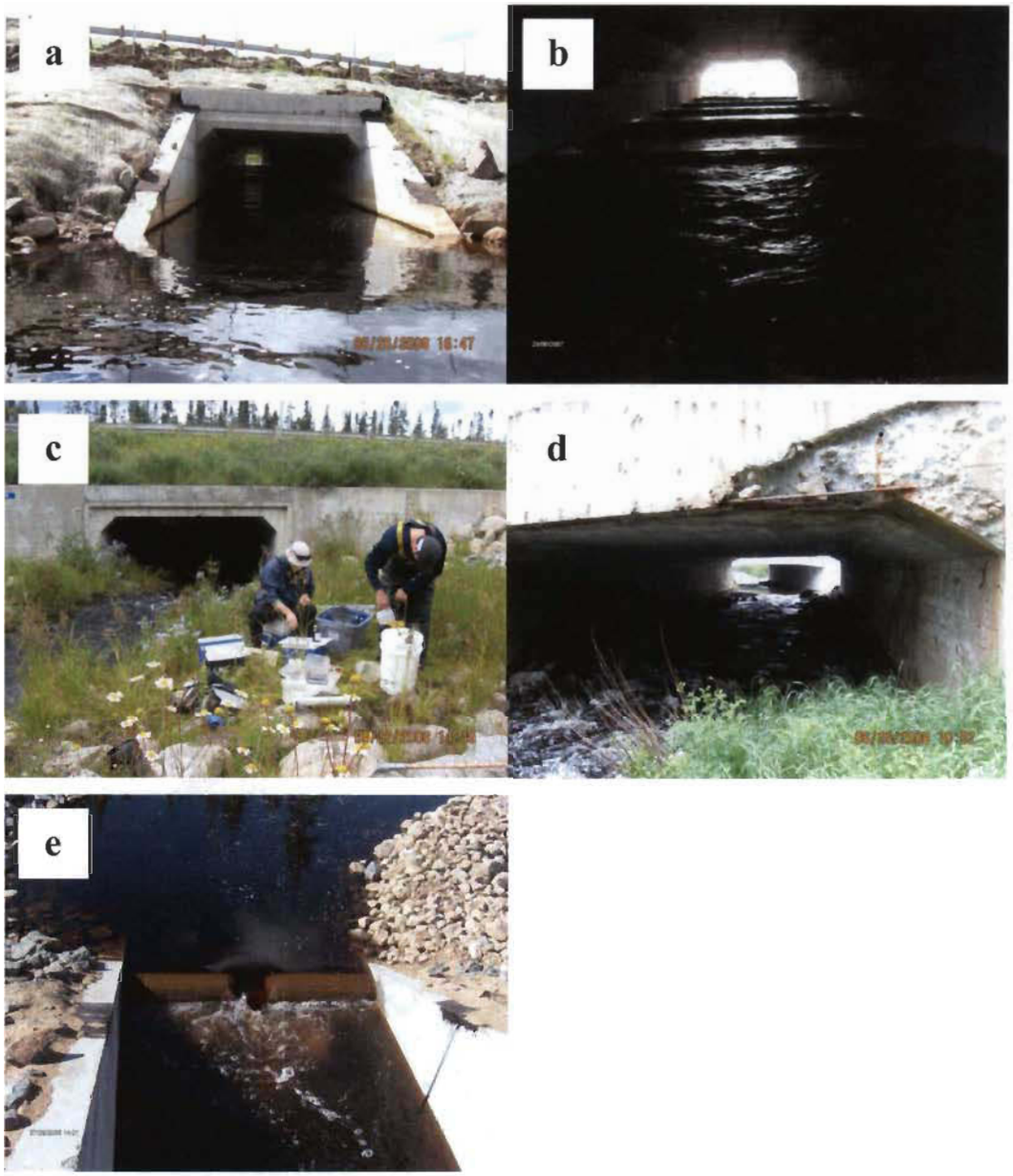

Figure A1

Appendix B. Extension of the Laplace barrier model to include a second barrier

Derivation of the probability density function of the Laplace model for the two-barrier case:

As in the single-barrier case, when multiple barriers are present the dispersal kernel is given by a mixture of components generated by traversal and reflection at the barriers. However, when more than a single barrier is present, the reflections generate an infinite series of components that must be summed to obtain the dispersal kernel. For the two-barrier case, the dispersal kernel $f_{2BL}(x,\delta,k_1,k_2)$ is given by:

$$f_0 + h_1(1-k_1)f_1 + \sum_{n=0}^{\infty} h_1 k_1^2 (1-k_2)^{n+1}(1-k_1)^n h_2^{2n+2} f_1, \qquad for\ x \le b_1$$

$$\sum_{n=0}^{\infty} h_1 k_1 (1-k_2)^n (1-k_1)^n h_2^{2n} f_1 + \sum_{n=0}^{\infty} h_1 k_1 (1-k_2)^{n+1}(1-k_1)^n h_2^{2n+1} f_2, \qquad for\ b_1 < x \le b_2$$

$$\sum_{n=0}^{\infty} h_1 k_1 k_2 (1-k_2)^n (1-k_1)^n h_2^{2n+1} f_2, \qquad for\ x > b_2$$

where

$$f_i = \frac{1}{2\delta}\exp\left(\frac{-|x-x_i|}{\delta}\right), \qquad i = 0, 1, 2$$

$$h_i = \exp\left(\frac{-|x_i - x_{i-1}|}{\delta}\right), \qquad i = 1, 2$$

$$x_0 = 0 < x_1 = b_1 < x_2 = b_2$$

The infinite series are convergent and their sum can be obtained analytically to yield:

$$f_0 + h_1(1-k_1)f_1 + \frac{h_1 h_2^2 k_1^2 (1-k_2)}{v} f_1, \qquad for\ x \le b_1$$

$$\frac{h_1 k_1}{v}\left(f_1 + h_2(1-k_2)f_2\right), \qquad for\ b_1 < x \le b_2$$

$$\frac{h_1 h_2 k_1 k_2}{v} f_2, \qquad for\ x > b_2$$

where

$$v = 1-(1-k_2)(1-k_1)h_2^2$$

which is a proper probability density function that integrates to 1. From this density function, likelihood-based estimation of parameters δ, k_1 and k_2 can proceed as in the single-barrier case.

Graphical representation:

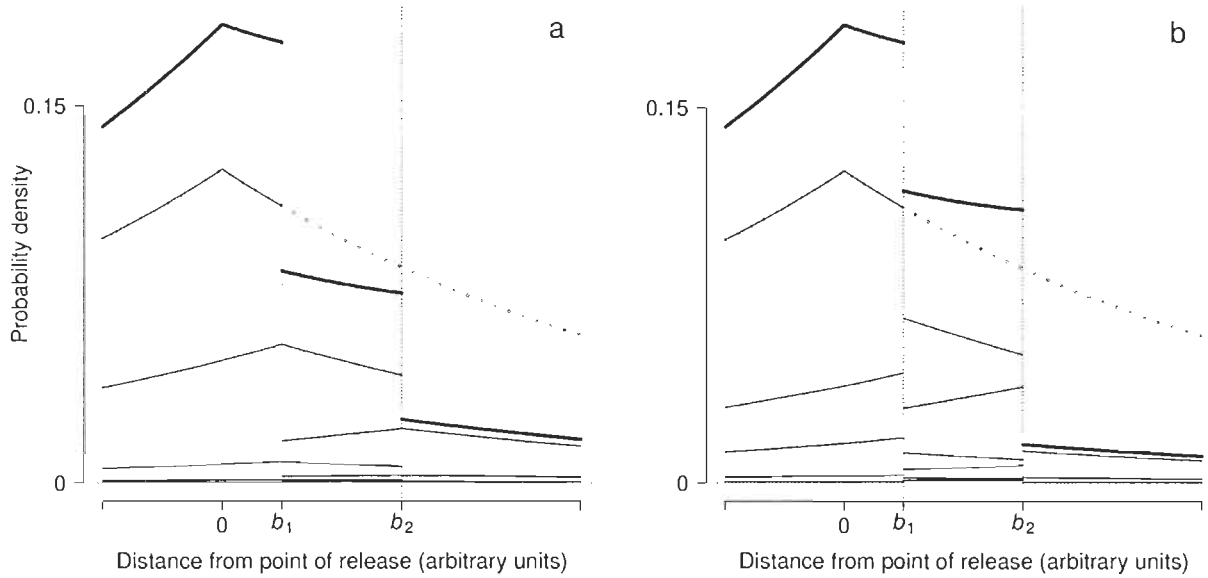

Figure B1. Examples of dispersal kernels (thick black curves) resulting from different combinations of barrier permeability when barriers are present at locations $x_1 = b_1$ (with permeability k_1) and $x_2 = b_2$ (with permeability k_2) and the point of release of a marked fish is at location $x_0 = 0$. a: $k_1 = 0.5$; $k_2 = 0.5$. b: $k_1 = 0.6$; $k_2 = 0.25$. In both cases, the dispersal parameter $\delta = 4$, $b_1 = 0.5$, $b_2 = 1.5$. The dispersal kernel in the absence of barrier effects ($k_1 = k_2 = 1$; dotted curves) and the kernel components generated by traversal and reflection at the barriers (thin black curves) are also shown. The dispersal kernel is given by the sum of the kernel components in each of three segments: $x \leq b_1$; $b_1 < x \leq b_2$; $b_2 < x$.

Appendix C

Longitudinal distribution of marked fish. The center of the highway is marked by vertical broken lines. Position relative to the highway is represented by negative (upstream) and positive (downstream) distances. The distribution of marked fish was used as an initial condition in the simulations of dispersal data. Streams are identified by milepost distance. n_0: number of marked fish.

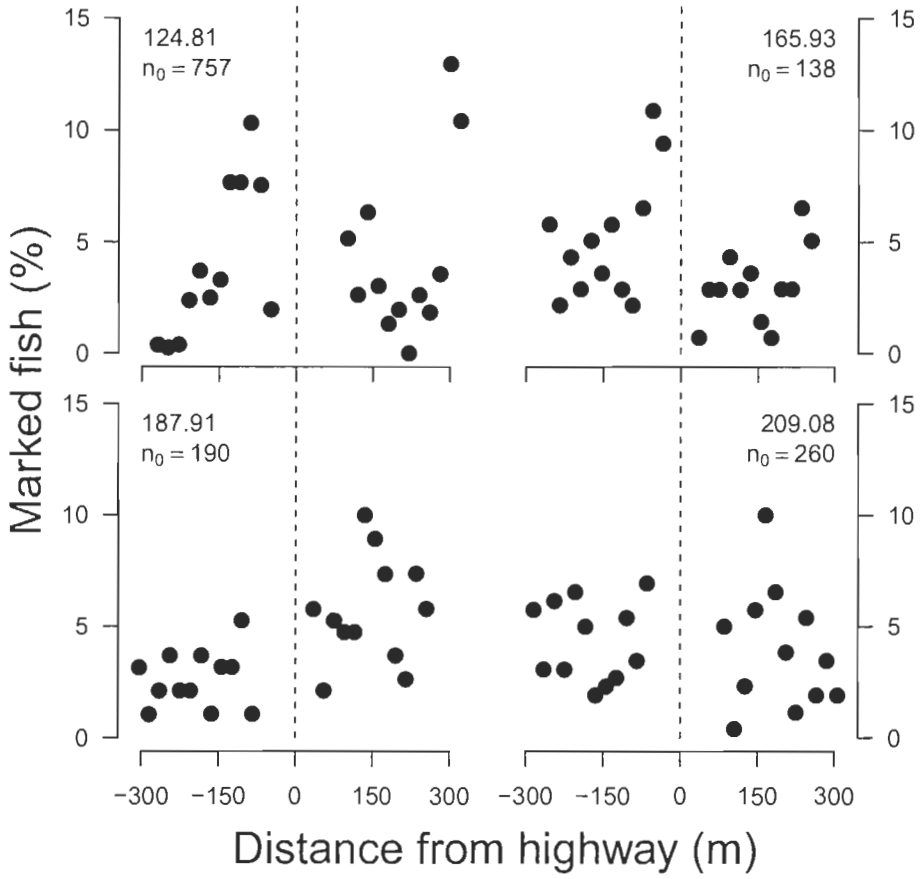
124.81
$n_0 = 757$
165.93
$n_0 = 138$
187.91
$n_0 = 190$
209.08
$n_0 = 260$
Marked fish (%)
Distance from highway (m)
0
5
10
15
−300
−150
0
150
300

Figure C1

Appendix D

Power to detect a barrier effect (% of simulations in which the 95% confidence interval for k did not include 1). Simulations for barrier Laplace mixture models were based on parameters estimated from field data (see Table 4), for five different values of k. Power to detect a barrier effect is presented for 100 and 1 000 simulation runs. Streams are identified by milepost distance.

k	Stream (milepost distance)							
	124.81		165.93		187.91		209.08	
	100	1000	100	1000	100	1000	100	1000
0.2	56	58	0	0	5	4	0	0
0.4	47	46	0	0	8	5	0	0
0.6	27	23	0	0	1	5	0	0
0.8	7	10	2	0	4	3	0	0
1.0	3	2	0	0	2	2	0	0

Appendix E

Estimates (circles) and 95 % confidence intervals (dots) of k in simulation runs for the barrier Laplace mixture models. Simulations were run for three values of δ_m (60, 300, and 1500 m), three sampling sizes (φN_0, $2\varphi N_0$, and $4\varphi N_0$), two highway widths (actual and 20 m), and five values of permeability k (0.2, 0.4, 0.6, 0.8, and 1.0). The proportion of stationary individuals ($p = 0.7$), mean dispersal of stationary individuals (δ_s = 10 m) and probability of recapture (φ = 0.4) were held constant for all simulations. Each plot comprises results from 100 simulation runs. The black and grey horizontal broken lines show the simulated k and the expected k in the absence of a barrier effect ($k = 1.0$), respectively. The black horizontal solid lines represent the estimated means of k. The black vertical bars represent 95% confidence intervals for the estimated means of k. Streams are identified by milepost distance.

Appendix E1: Stream 124.81

Appendix E2: Stream 165.93

Appendix E3: Stream 187.91

Appendix E4: Stream 209.08

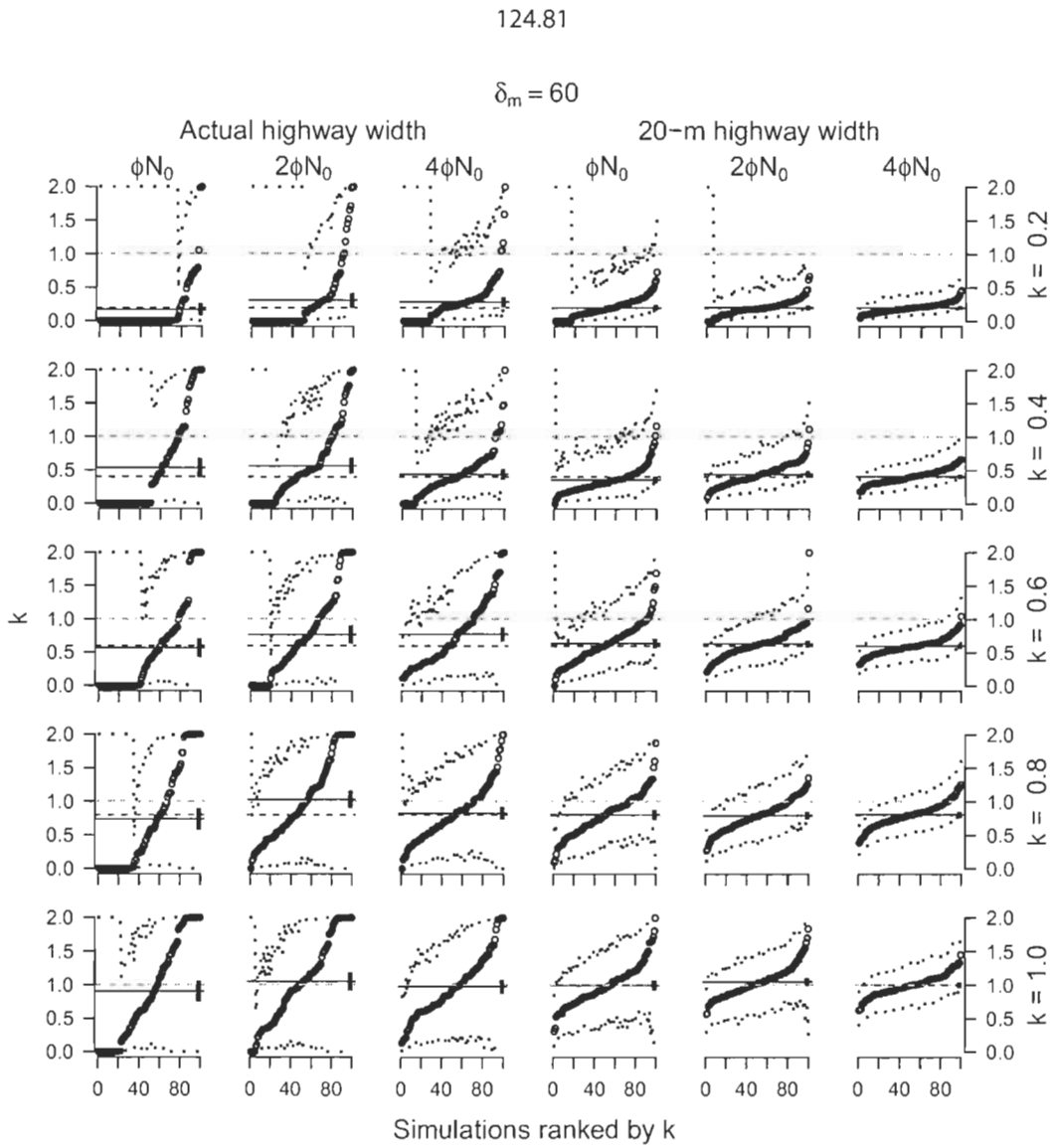
124.81
$\delta_m = 60$
Actual highway width
20−m highway width
ϕN_0
$2\phi N_0$
$4\phi N_0$
k = 0.2
k = 0.4
k = 0.6
k = 0.8
k = 1.0
k
Simulations ranked by k

Figure E1

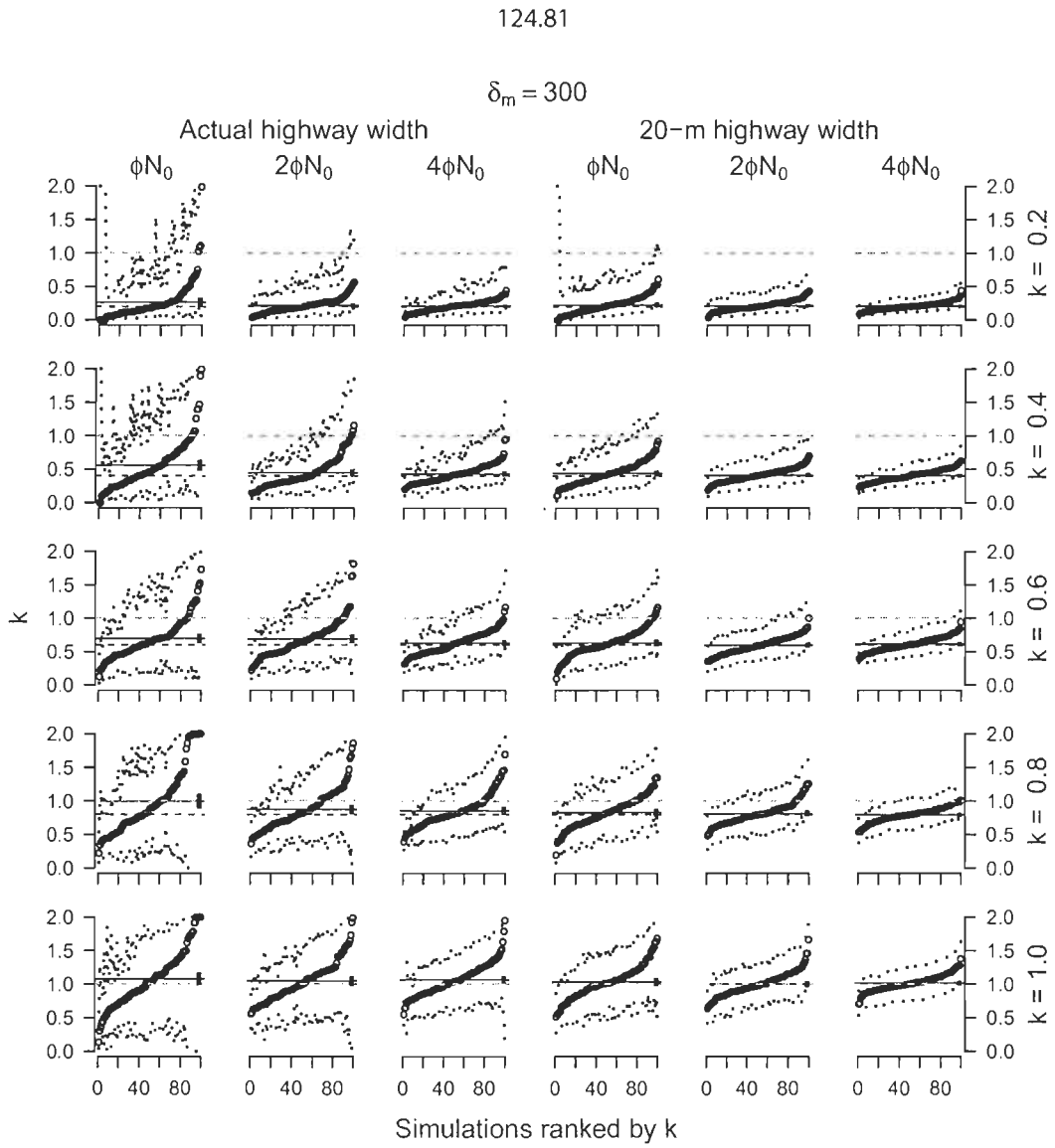
124.81
$\delta_m = 300$
Actual highway width
20−m highway width
ϕN_0
$2\phi N_0$
$4\phi N_0$
k = 0.2
k = 0.4
k = 0.6
k = 0.8
k = 1.0
k
0.0
0.5
1.0
1.5
2.0
0
40
80
Simulations ranked by k

Figure E1

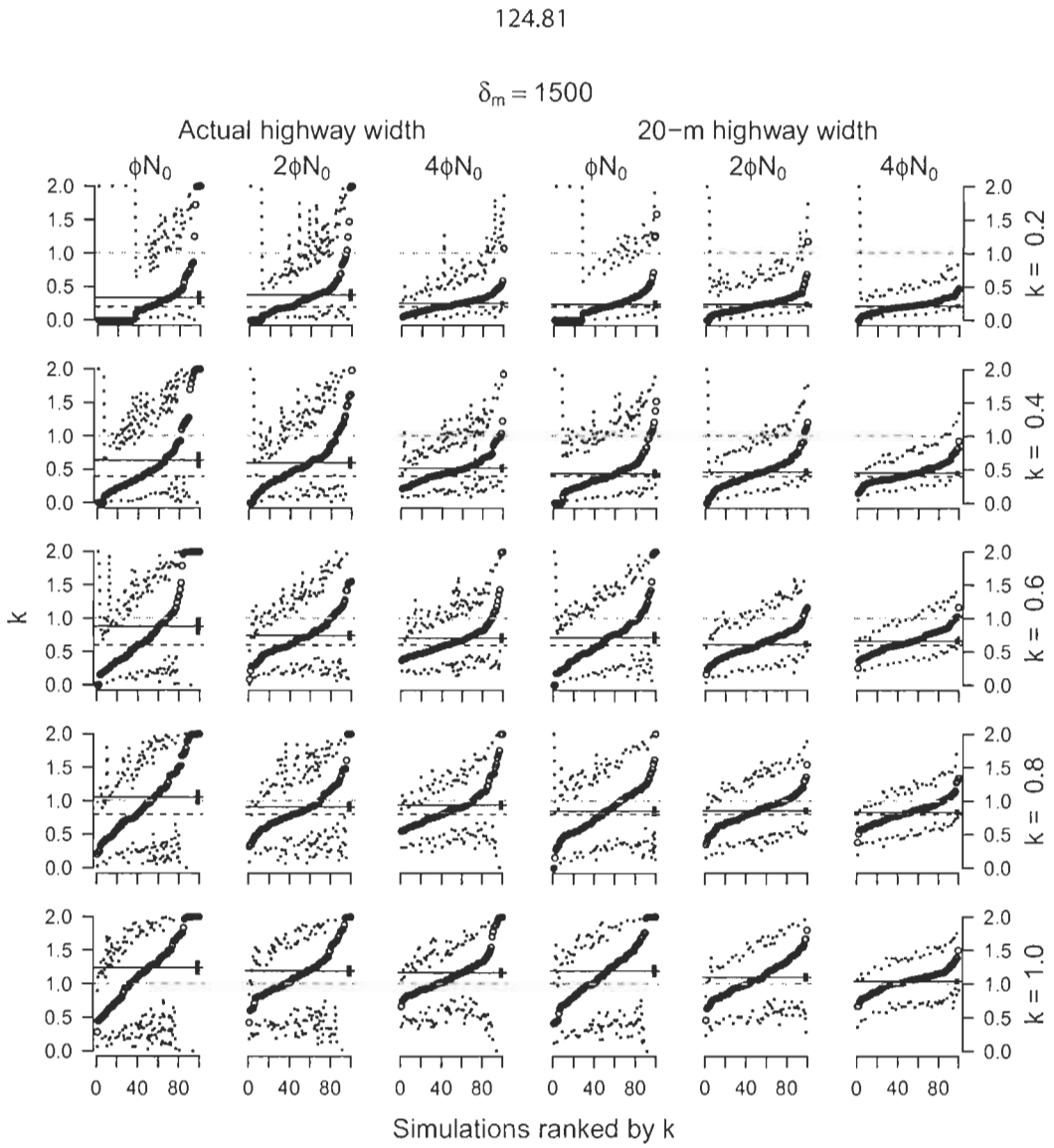
124.81
$\delta_m = 1500$
Actual highway width
20−m highway width
ϕN_0
$2\phi N_0$
$4\phi N_0$
k = 0.2
k = 0.4
k = 0.6
k = 0.8
k = 1.0
k
Simulations ranked by k

Figure E1

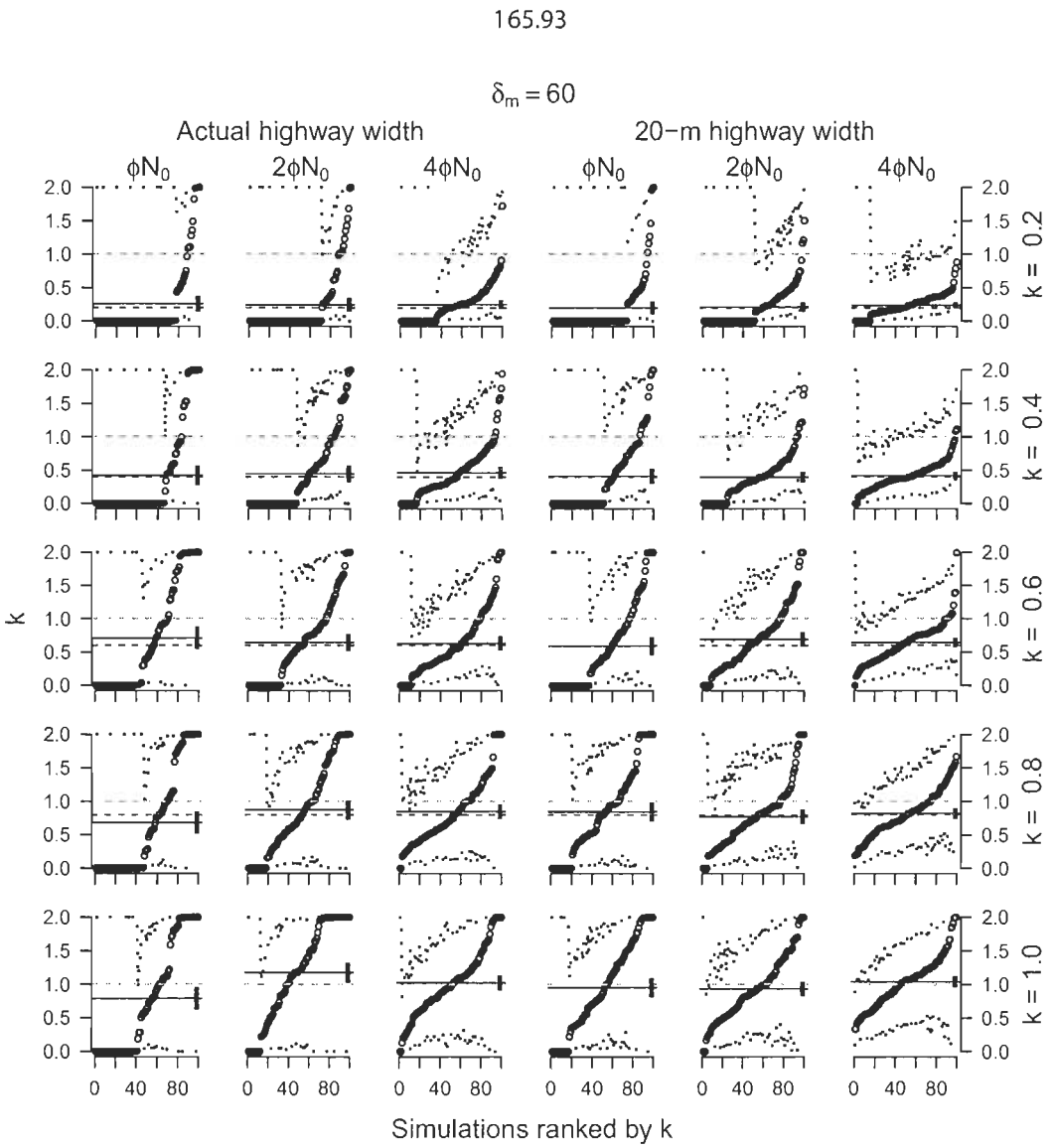
165.93
$\delta_m = 60$
Actual highway width
20−m highway width
ϕN_0
$2\phi N_0$
$4\phi N_0$
k = 0.2
k = 0.4
k = 0.6
k = 0.8
k = 1.0
k
Simulations ranked by k

Figure E2

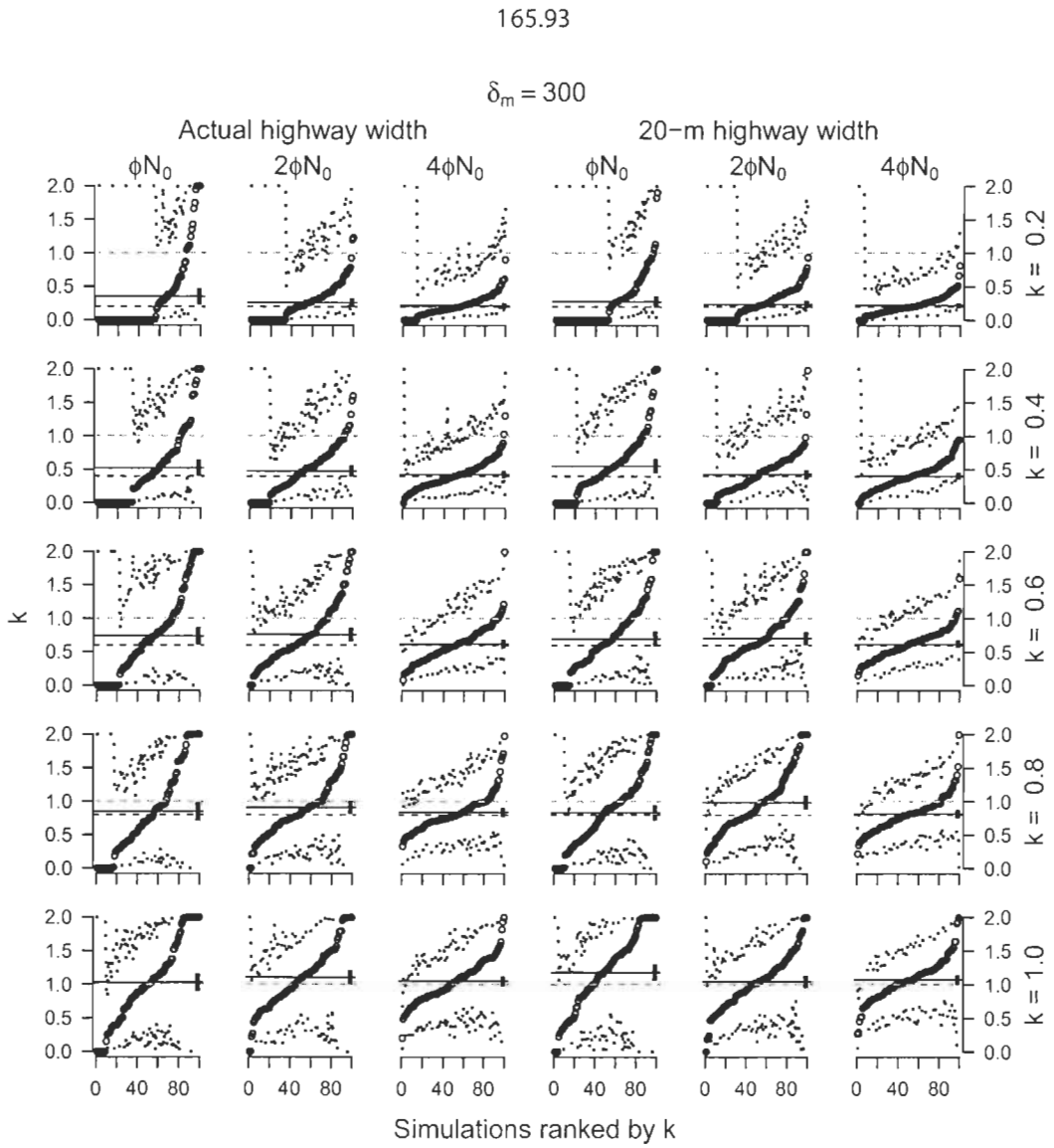
165.93
$\delta_m = 300$
Actual highway width
20−m highway width
ϕN_0
$2\phi N_0$
$4\phi N_0$
k = 0.2
k = 0.4
k = 0.6
k = 0.8
k = 1.0
k
Simulations ranked by k

Figure E2

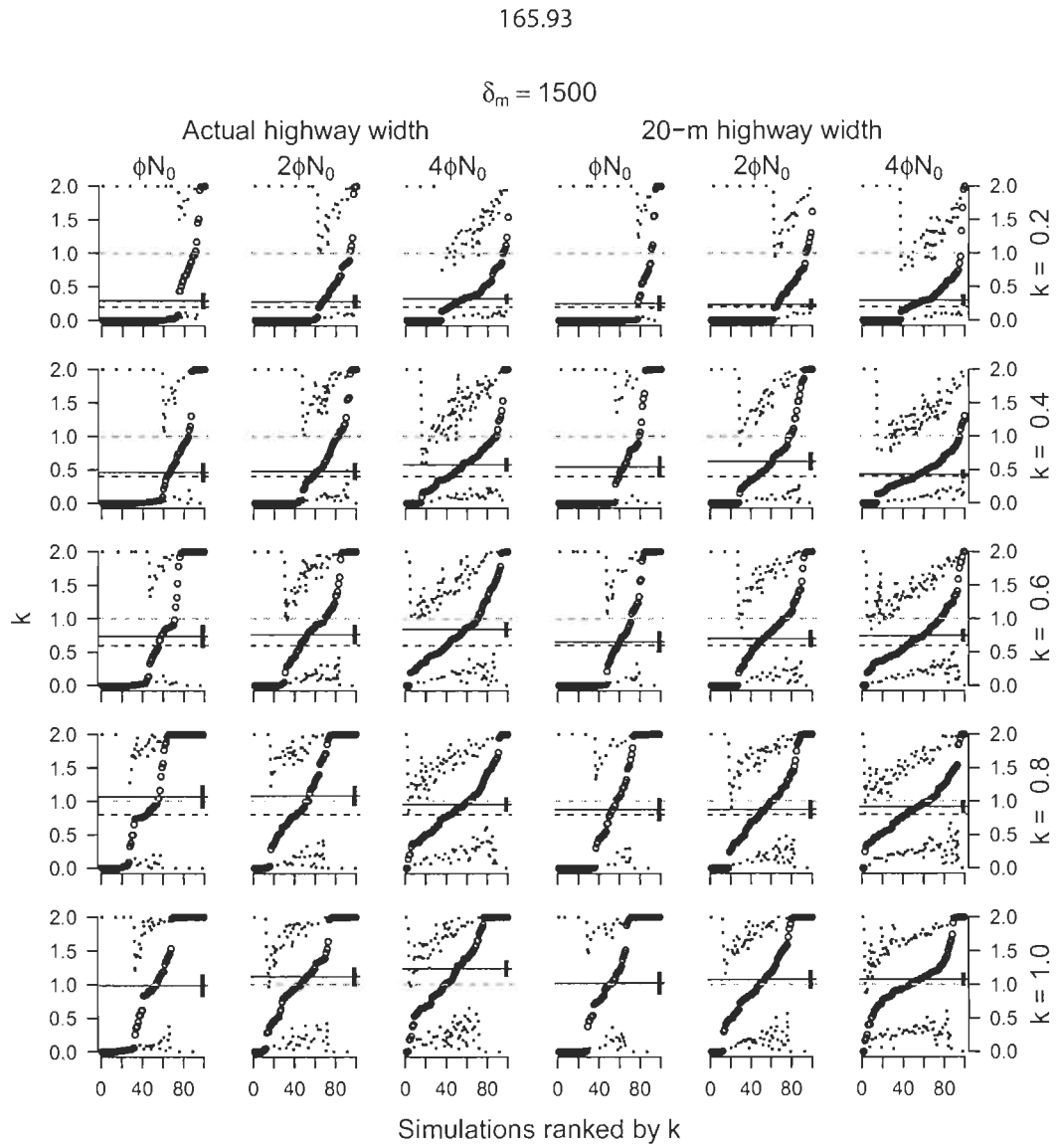
165.93
δ_m = 1500
Actual highway width
20−m highway width
ϕN_0
$2\phi N_0$
$4\phi N_0$
k = 0.2
k = 0.4
k = 0.6
k = 0.8
k = 1.0
k
0.0
0.5
1.0
1.5
2.0
0
40
80
Simulations ranked by k

Figure E2

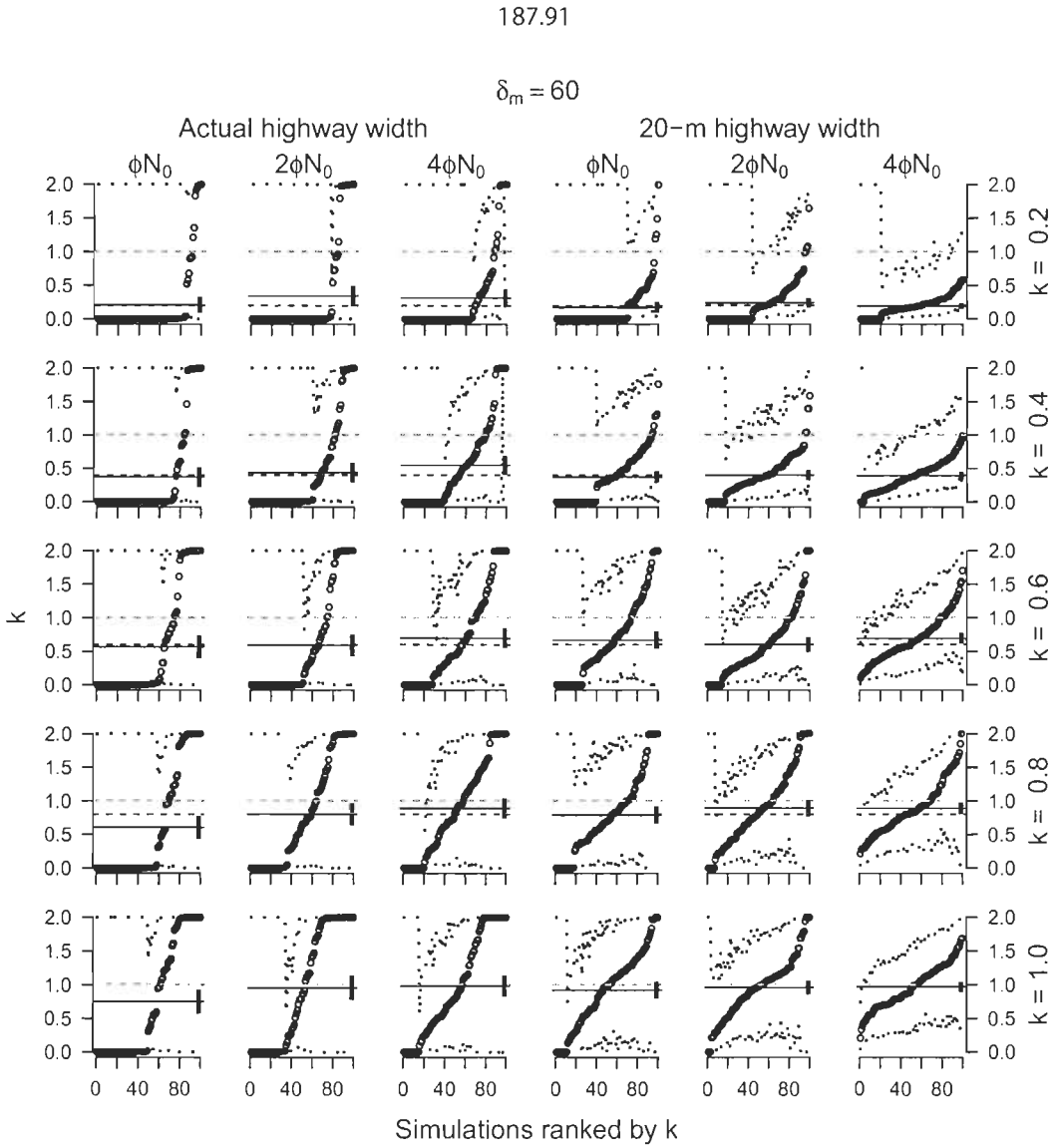
187.91
$\delta_m = 60$
Actual highway width
20−m highway width
ϕN_0
$2\phi N_0$
$4\phi N_0$
k
k = 0.2
k = 0.4
k = 0.6
k = 0.8
k = 1.0
0.0
0.5
1.0
1.5
2.0
0
40
80
Simulations ranked by k

Figure E3

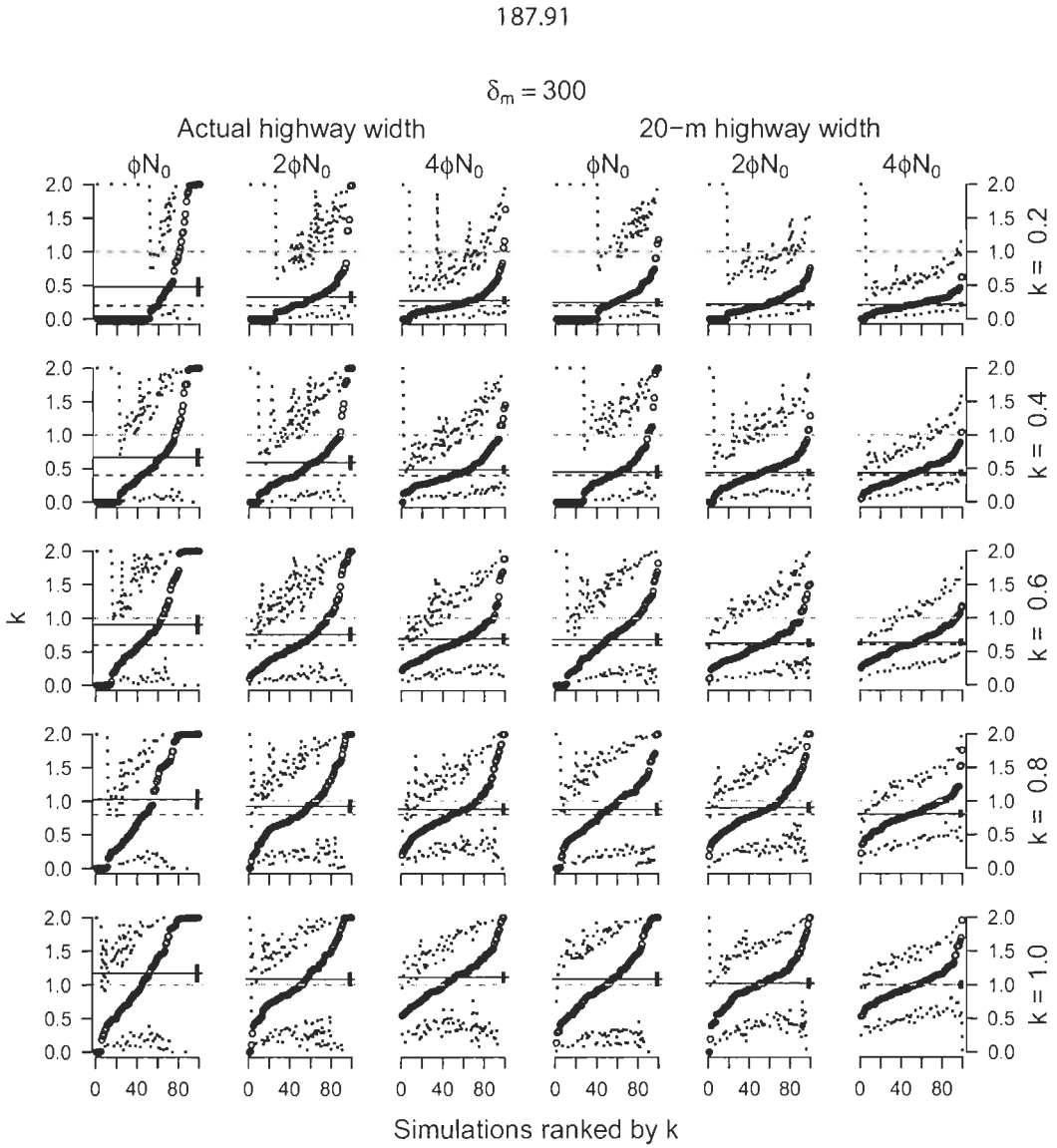
187.91
$\delta_m = 300$
Actual highway width
20−m highway width
ϕN_0
$2\phi N_0$
$4\phi N_0$
k = 0.2
k = 0.4
k = 0.6
k = 0.8
k = 1.0
k
Simulations ranked by k

Figure E3

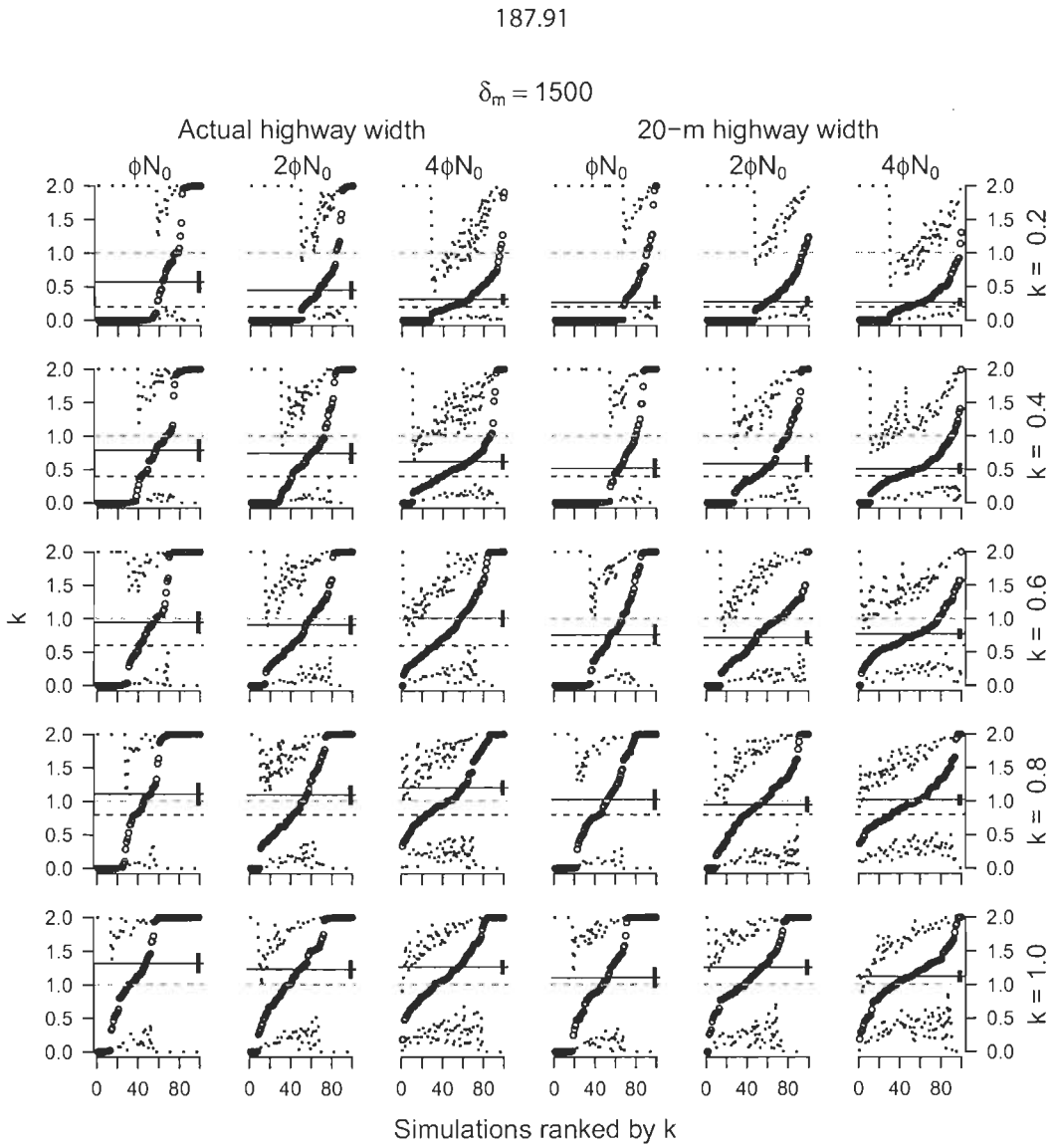
187.91
$\delta_m = 1500$
Actual highway width
20−m highway width
ϕN_0
$2\phi N_0$
$4\phi N_0$
k
k = 0.2
k = 0.4
k = 0.6
k = 0.8
k = 1.0
0.0
0.5
1.0
1.5
2.0
0
40
80
Simulations ranked by k

Figure E3

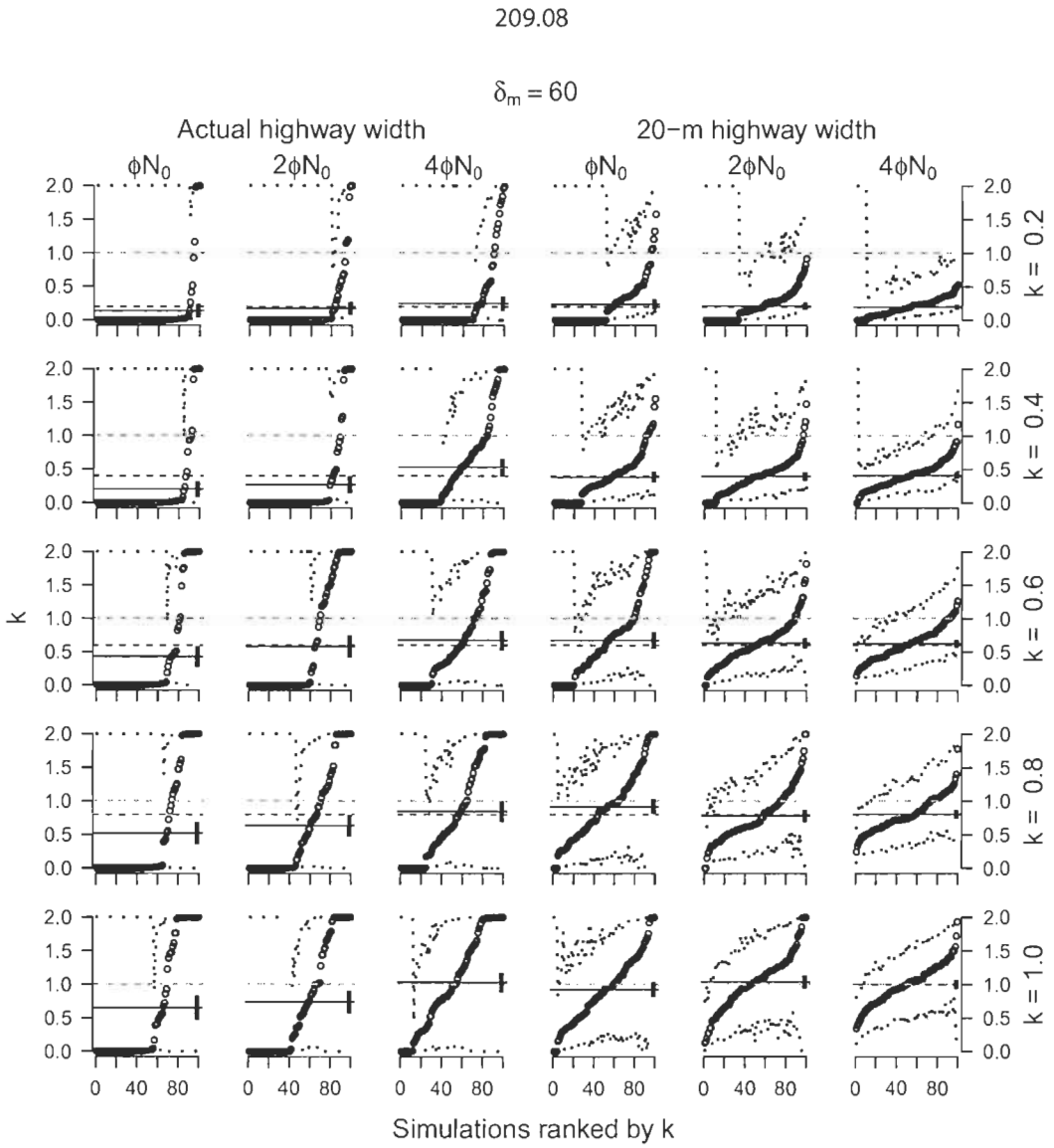
209.08
$\delta_m = 60$
Actual highway width
20−m highway width
ϕN_0
$2\phi N_0$
$4\phi N_0$
k = 0.2
k = 0.4
k = 0.6
k = 0.8
k = 1.0
k
Simulations ranked by k

Figure E4

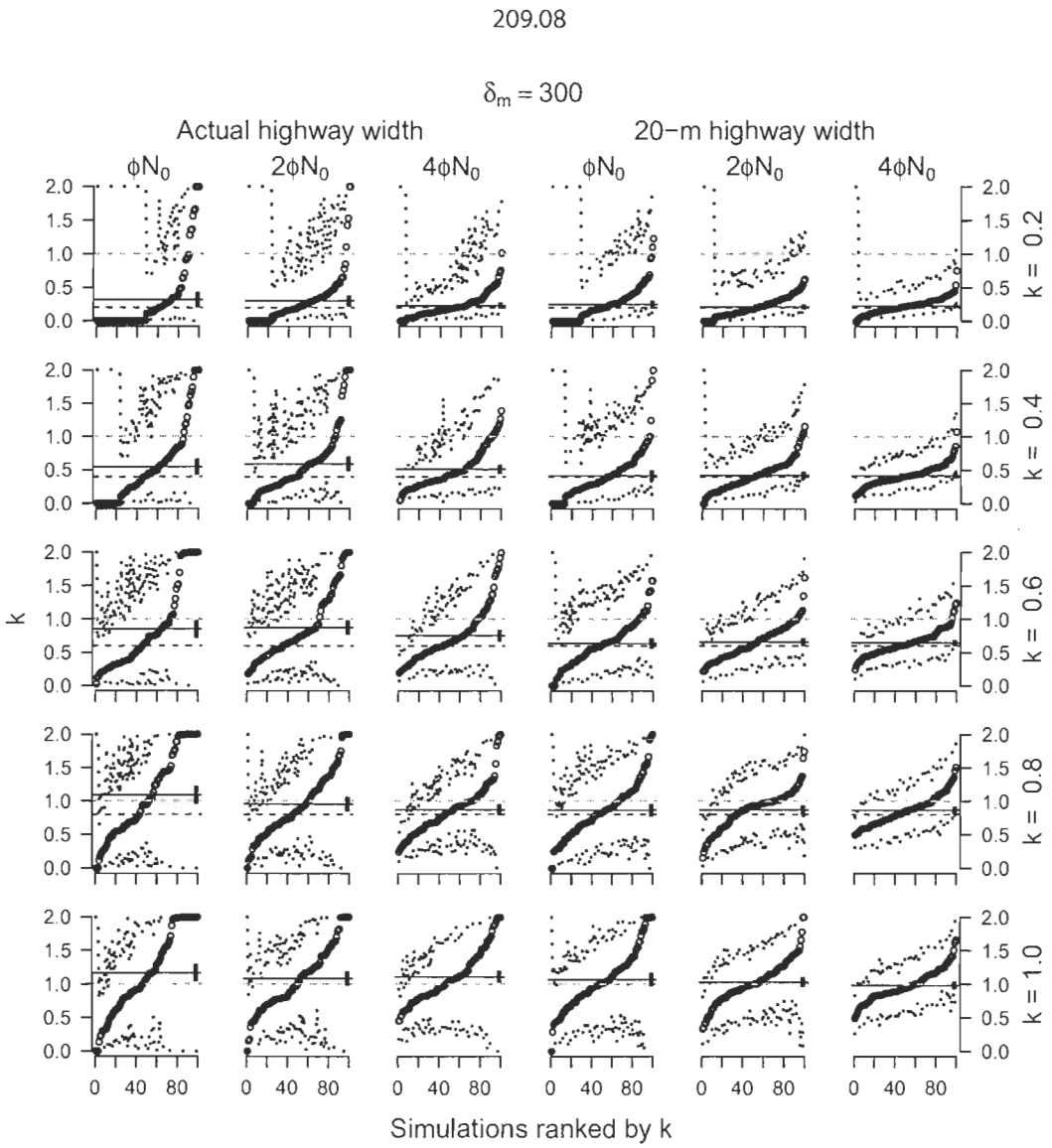
209.08
$\delta_m = 300$
Actual highway width
20−m highway width
ϕN_0
$2\phi N_0$
$4\phi N_0$
k = 0.2
k = 0.4
k = 0.6
k = 0.8
k = 1.0
k
Simulations ranked by k

Figure E4

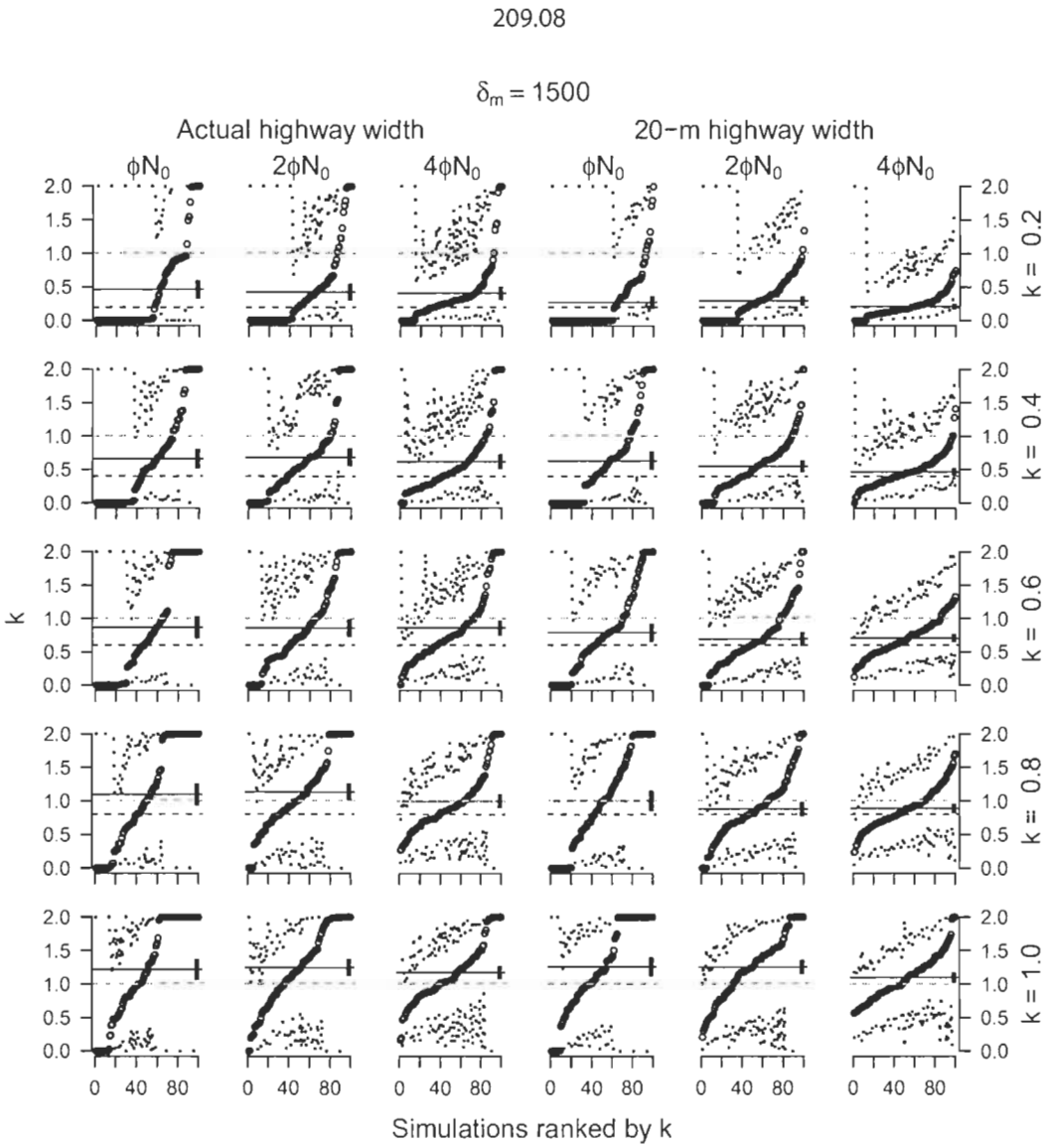
209.08
δ_m = 1500
Actual highway width
20−m highway width
ϕN_0
$2\phi N_0$
$4\phi N_0$
k = 0.2
k = 0.4
k = 0.6
k = 0.8
k = 1.0
k
Simulations ranked by k

Figure E4

CHAPITRE III

IMPACTS OF HIGHWAY CONSTRUCTION ON REDD COUNTS OF STREAM-DWELLING BROOK CHARR

Marc Pépino, Jan Franssen, Marco A. Rodríguez and Pierre Magnan

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Voice: (819) 376 5011 ext. 3375
Fax: (819) 376 5084

Résumé

La sédimentation, particulièrement pendant la construction routière, est un impact induit par l'homme qui menace les écosystèmes aquatiques. Malgré une littérature abondante sur les effets des sédiments fins sur les premiers stades de développement des poissons, nous n'avons pas connaissance d'études qui ont investigué le retour des géniteurs sur les sites de reproduction dans les cours d'eau impactés par une construction routière. L'objectif de cette étude était de quantifier le retour sur les sites de reproduction d'ombles de fontaine à différents stades d'avancement de la construction autoroutière (avant, pendant, et après construction). Le dénombrement des nids a été réalisé à une résolution spatiale fine (< 0.5 m) pendant deux années consécutives dans 12 tronçons distribués le long d'un parcours linéaire d'autoroute de 115-km dans la réserve faunique des Laurentides, Québec (Canada). Nous avons trouvé une diminution significative du nombre de nids dans les tronçons affectés par la construction pendant la seconde année, mais aucune évidence d'impacts dans les tronçons affectés par la construction pendant la première année. Une explication parcimonieuse pourrait être que les libérations de sédiments étaient bien contrôlées pendant la construction sauf après un évènement météorologique extrême survenant pendant la saison de reproduction de la seconde année. Cependant, nous avons observé qu'un tronçon lourdement impacté par les sédiments supportait toujours de hautes densités de géniteurs. Dans l'ensemble, nous avons démontré que les nombres de nids étaient stables entre les deux années, à la fois à l'intérieur et entre les tronçons et quels que soient l'état d'avancement de la construction autoroutière ou la charge sédimentaire, ce qui suggère que le retour des géniteurs est davantage contraint par des variables de l'habitat que par la construction autoroutière.

Mots-clés : écologie des routes ; évaluation des impacts environnementaux ; évènement météorologique extrême ; reproduction ; sédiment ; *Salvelinus fontinalis*

Abstract

Sedimentation, particularly during road construction, is a human impact that threatens aquatic ecosystems. Despite a large body of literature on the effect of fine sediments on the initial developmental stages of fishes, we do not know of any studies that have investigated the return of spawners to spawning grounds in streams impacted by road construction. The objective of this study was to quantify the return to spawning grounds of brook charr at different stages of highway construction (before, during, and after construction). Redd counts were made at a fine spatial resolution (< 0.5 m) over two consecutive years in 12 reaches distributed along a 115-km stretch of highway in the Laurentides Wildlife Reserve, Québec (Canada). We found a significant decrease in redd counts in reaches affected by construction during the second year, but no evidence of impacts in reaches affected by construction during the first year. A parsimonious explanation could be that sediment releases were well controlled during construction except after an extreme weather event occurring during the spawning season of the second year. However, we observed that a reach heavily impacted by sediments still supported high densities of spawners. Overall, we showed that redd counts were stable between the two study years, both within and among reaches and for all stages of highway construction and sediment loadings, which suggests that the return of spawners is more constrained by habitat variables than by highway construction.

Key-words: environmental impact assessment; extreme weather event; road ecology; sediment; spawning; *Salvelinus fontinalis*

Introduction

Sedimentation is a human impact that threatens aquatic ecosystems (Waters 1995; Sutherland et al. 2002; Kemp et al. 2011) and is a growing concern due to expanding land use and climate change (Scheurer et al. 2009). Sediment transport and deposition are especially problematic in streams during road construction because of erosion and alteration of the hydrologic network at intersections with roads, resulting in higher peak flows and sedimentation (Forman & Alexander 1998; Jones et al. 2000; Benda et al. 2004; Wheeler et al. 2005). Currently, measures to mitigate bank erosion are not entirely effective and sedimentation still remains a concern (Shields 2009; Collins et al. 2010). Therefore, it is important to assess the ecological impacts of increased sedimentation before, during, and after road construction. Fish species that require clean gravel substratum for spawning are thought to be the most affected by sedimentation (Sutherland et al. 2002; Scheurer et al. 2009).

Salmonid species are very sensitive to fine sediments (Chapman 1988; Lisle 1989; Jensen et al. 2009). Most studies on the impacts of sediments on salmonids have focused on the initial developmental stages, from egg deposition to emergence (Bernier-Bourgault & Magnan 2002; Julien & Bergeron 2006; Guillemette et al. 2011). The mechanisms proposed to explain the decrease in survival-to-emergence in the presence of fine sediments are reduction of oxygenated water supply to embryos (Greig et al. 2005; Heywood & Walling 2007) and restriction of free movement at emergence (MacCrimmon & Gots 1986; Fudge et al. 2008; Sternecker & Geist 2010; Franssen et al. 2012). Despite the large body of literature on the effect of fine sediments on the initial developmental stages of fishes, we do not know of any studies that have investigated the return of spawners to spawning grounds impacted by fine sediments. More specifically, road construction can 1) reduce the amount of suitable habitat for spawning due to sedimentation (Alexander & Hansen 1986; Magee et al. 1996) and 2) cause gill damage due to increased water turbidity (Berg &

Northcote 1985; Lazar et al. 2010). In both cases, a reduction in spawner abundance is expected (spawners can move outside the zone of influence of highway construction, or decide to spawn in other reaches). Cumulative effects of emergence success and spawner avoidance could result in a decline of stream-dwelling populations near roads. For example, Baxter et al. (1999) reported a negative correlation between number of redds and density of forest roads.

The objective of this study was to quantify the spawning return of brook charr, *Salvelinus fontinalis*, in relation to the stage of highway construction (before, during, and after construction). More specifically, we predicted a reduction in the number of spawners occurring in reaches under highway construction. We used redd count as an index of spawner abundance and reported changes in spawner distribution at fine spatial resolution (< 0.5 m) within reaches spread along a 115-km stretch of highway.

Material and Methods

Study area

The study was carried out in 12 streams of the Laurentides Wildlife Reserve (47° 45'N, 71° 15'W), Québec (Canada), which is located on the Laurentian Plateau at altitudes between 360 and 820 m (Fig. 1). The area has humid continental climate with harsh winters (mean annual temperature: 0.3 °C; annual snowfall: 639 cm). Vegetation cover is continuous boreal forest dominated by balsam fir, *Abies balsamea*, and white birch, *Betula papyrifera*. Watershed geology is largely homogeneous and consists of a metamorphic basement (gneiss) with intrusive rocks (mainly mangerites); stream formation is primarily by glacial deposits and outwash. The annual discharge regime has a dominant peak in the spring at snowmelt and seasonal lows in late summer.

Highway 73/175, which runs between Québec and Saguenay cities (Québec, Canada), was built in 1948. A major construction project, undertaken during the period 2006 – 2012, widened the highway from two to four traffic lanes. The mean width of the highway's "zone of influence", which includes the traffic lanes and all areas required for road security and maintenance, such as ditches and additional strips of land, increased from 30 m to 120 m. Measures implemented to reduce sedimentation during construction included use of erosion control mattresses to stabilize stream banks, gravel filters placed along construction ditches to promote sedimentation and geotextile curtains to limit dispersal of suspended particulate matter. The highway is the only apparent source of human disturbance on the aquatic environment in the Laurentides Wildlife Reserve.

We selected 12 reaches along a 115-km stretch of the highway to estimate the spawning abundance of brook charr in 2007 and 2008 (Table 1). The reaches cover essentially the first 500 m of the streams on each side of the highway (Fig. 2). These reaches are in small tributaries (Strahler order 1–3; Table 1), have a median slope of 2.5% (range 0.3–12.8%; Table 1) and a gravel bed substrate; these features provide suitable habitat for the reproduction of brook charr (Witzel & MacCrimmon 1983; Kondolf & Wolman 1993; Curry et al. 2002). Underwater visibility was high and allowed for observation of spawning.

Redd counts

Each reach was visited weekly to count the number of redds in 2007 (5 September to 17 October) and 2008 (15 August to 19 October). The visits began prior to spawning season and continued until the end of the spawning season (see Results section). During a visit, redds were counted by walking slowly in an upstream direction along the stream bank. When a potential redd was detected, the observer would crouch down and wait for at least three minutes to check for the presence of

spawners. The observer was equipped with polarized sunglasses, and visits were always conducted in high visibility conditions to ensure consistency in the detection of redds. Redds were confirmed by the observation of a clearly defined nest (disturbed streambed sediments with a characteristic pit tailspill formation), an actively digging female, or a male fighting for a stationary female (Crisp & Carling 1989; Blanchfield & Ridgway 1999). The longitudinal position of each redd was recorded (nearest 0.5 m) using a measuring tape and flags spaced at 20-m intervals. The center of the highway was defined as the origin of the longitudinal position. Upstream and downstream locations were assigned negative and positive distances from the origin, respectively. The same observer identified redds following this protocol in 2007 and 2008.

Sediment and water level data

Sediment traps were used to determine the magnitude and duration of fine sediment increase resulting from highway construction. Two to four traps (depending on stream width) were installed in six reaches at downstream locations (Table 1). The sediment trap consisted of a bucket set into the streambed, incorporating a void space and nested in a slightly larger bucket (for ease of replacement; Lisle 1989). Buckets were installed with their rims 2.5 cm above the streambed to avoid excess collection of bedload. In reach 94.59, the streambed could not be excavated to install the usual bucket-type trap because of obstruction by large boulders and bedrock. Thus, we built a sediment trap consisting of a hollow collection tube that was closed at one end and secured within a concrete block anchored to the streambed. Both types of sediment traps were removed and replaced (hereafter reset) with an empty trap at regular time intervals (two to four weeks) from May 2006 to October 2009. Trap contents were dried and sieved for particle size analysis using standard methods (ASTM 2006). We considered fine sediments as the total mass of sediments < 0.5 mm in diameter.

The upstream section of reach 143.75 was instrumented with a permanent recording station that monitored water level using a Submersible Pressure Transducer (range: 0–2 m; accuracy: 0.25% static; Keller America, Inc.). Sediment and water level data originated from a complementary project and were not designed to fit with the spawning records presented here. No statistical analyses were done with fine sediments or water level data because of the lack of replication, but graphical analyses were used to interpret the impacts of highway construction on redd counts.

Statistical analyses

Depending on the reach, highway construction occurred during the first year (thus yielding a "during–after" study period; n = 4), the second year (a "before–during" study period; n = 5), or not at all (a "before–before" study period; n = 3). This classification was used to define a three-level treatment variable (Table 1). Since we had two years of observations, the impacts of highway construction were analyzed by one-way ANOVA with the difference in redd counts between 2007 and 2008 as the response variable and the treatment as the fixed factor (Green 1993). Group-wise differences were assessed with a post-hoc Tukey test.

The spatial distribution of redds within each reach was estimated by kernel density functions, a form of smoothing curves that provide a continuous approximation to the underlying data distribution (Silverman 1986). The bandwidth of the kernel density was set to 12.5 for all distributions for consistence in the comparison of spatial distributions of redds between years and among reaches. This bandwidth provided a suitable compromise that avoided over- and under-smoothing of the spatial distributions of redds. All analyses were done in the R environment (R Development Core Team 2010).

Results

The spawning season lasted from 5 September until 17 October 2007 and from 23 August to 19 October 2008 (Fig. 3). The timing of arrival of spawners on their spawning ground was consistent between the two years, with the peak of redd counts occurring the last week of September (Fig. 3). Redds were always observed in the 12 reaches for both years (Table 1). Overall, redd counts were higher in 2008 (n = 551) than in 2007 (n = 450). The water level was on average higher in 2008 than in 2007 (Fig. 3).

The one-way ANOVA of differences in redd counts revealed a significant effect of the treatment ($F_{2,9} = 4.263$, $P < 0.05$). A post-hoc Tukey test indicated that the only significant difference was between before–before and before–during treatments ($P < 0.05$). Redd counts increased from 2007 to 2008 in all reaches of the before–before and during–after treatments whereas redd counts decreased from 2007 to 2008 in four out of five reaches of the before–during treatment (Fig. 4). The spatial distribution of redds within reaches was stable and consistent between years regardless of the stage of highway construction (Fig. 5). More specifically, the reaches that received many spawners during the first year, continued to receive many spawners during the second year (e.g. reaches 94.59, 96.37, 104.67, 161.70; Fig.5). The spawning aggregations occurred within 200-m reach lengths.

Among the six reaches where fine sediments were collected, a major increase of fine sediments occurred in reach 96.37 during the 2008 spawning season (Fig. 6). This increase corresponded to a documented extreme weather event, tropical cyclone Ike (Environment Canada archives 2011), which occurred in the area in mid-September and resulted in very high peak flow (Fig. 3); more than 50 mm of precipitation fell within the area in less than six hours (Environment Canada archives 2011). No other reach collecting fine sediment data was in construction during this

event, which limits inference to other reaches in construction during this event. However, neither reaches that were not in construction in the 2008 spawning season nor other reaches outside the 2008 spawning season were affected by fine sediments (Fig. 6).

Discussion

To our knowledge, this is the first study quantifying the impact of different stages of highway construction on return of spawners. Overall, the increase in redd count observed in undisturbed reaches in 2008 (44% on average) could have been the result of: (1) higher discharge during the spawning periods and subsequent increase in the ability of spawners to migrate (Taylor et al. 2010); or (2) natural variability. Controlling for this variability (Green 1993), our results showed that highway construction induced a significant decrease in redd count in reaches under construction in 2008 (i.e. 3 % on average), but there was no evidence of impacts in reaches under construction in 2007. A parsimonious explanation could be that sediment releases were well controlled during construction except after an extreme weather event, tropical cyclone Ike, which occurred during the spawning season of the second year. The decrease in redd count might have been caused by increase in water turbidity, which influences spawners during migration (Whitman et al. 1982; Servizi & Martens 1992), or to the unavailability of clean gravel substratum for spawning (Kondolf & Wolman 1993; Magee et al. 1996).

Highway construction impacts were reported on short temporal scales and on local spatial scales (i.e., within the first kilometres of the highway). In addition, sediment data showed a rapid return (< one year) to their initial levels after impacts, perhaps because of rapid sediment turnover in headwater streams (Verstaeten et al. 2007; Lachance et al. 2008), suggesting that highway construction can affect spawning sites on short temporal scales near the highway. However, at the landscape

scale, the accumulation of sediments in the watershed has been shown to induce dramatic changes in aquatic ecosystems (Waters 1995; Sutherland et al 2002; Donohue & Molinos 2009). For example, the accumulation of sediments in lakes can modify the ecological processes and restructure energy flow pathways; these modifications frequently result in reduced biological diversity and productivity (Donohue & Molinos 2009). Thus, future investigations should evaluate sediment effects on population dynamics at the watershed scale to ensure that the observed effects were not underestimated at larger spatial scales (Fausch et al. 2002; Harvey & Railsback 2009; Scheurer et al. 2009).

Contrary to our prediction, the reach heavily impacted by fine sediments (reach 96.37; 1 800 % increase in fine sediments on average; Fig. 6) still supported a high return of spawners (Figs 4 & 5). Although we had no evidence of the completion of spawning, active reproductive behaviours (e.g. female digging and male combat) were observed in this reach during the 2008 spawning season (Video Clip S1, Supporting Information). In this context, we suggest that the return of spawners in degraded habitats will result in a reduction of individual fitness due to fine sediment accumulation in the substrate (Bernier-Bourgault & Magnan 2002; Jensen et al. 2009; Guillemette et al. 2011). This in turn could lead to population decline (Alexander & Hansen 1986; Nakamura et al. 1994; Baxter et al. 1999).

Highway construction led to few modifications in the return of spawners. The observed stability of the spawning sites between the two years, both within and among reaches and at all stages of highway construction and levels of sediment loading, suggests that spawning areas are determined by habitat features. Therefore, the development of tools that predict the spawning areas from habitat variables should help managers identify and protect critical fish habitats from human disturbances, as has been proposed for some salmonid species in other contexts (Steel et al. 2004; Poplar-Jeffers et al. 2009).

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Table 1. Redd counts, stream characteristics, and number of sediment traps for the 12 reaches along Highway 73/175 in the Laurentides Wildlife Reserve (Québec, Canada). Three treatment-level variables summarize the stage of highway construction between 2007 and 2008: BB ("before–before"), BD ("before–during"), and DA ("during–after"). Reaches are identified by milepost distance from south (km 94.59) to north (km 209.08)

Reach	Strahler order	Width (m)	Slope (%)	Number of traps	Treatment	Redd count	
						2007	2008
94.59	2	5.7	4.0	3	DA	125	143
96.37	1	1.3	12.8	2	BD	54	49
101.63	1	1.1	3.3	0	BD	9	5
104.10	1	2.9	2.7	0	BD	29	29
104.67	1	3.5	1.4	0	BD	110	95
113.32	1	1.9	2.3	0	DA	6	9
133.11	2	3.1	1.0	3	DA	10	31
143.75	2 – 3	5.2	0.3	4	BB	14	36
161.70	2	1.9	1.1	2	BB	58	89
165.93	1	1.8	2.0	2	BB	25	35
174.33	1	1.4	3.1	0	BD	5	22
209.08	2	2.5	2.6	0	DA	5	8

Figure legends

Figure 1. Localisation of the 12 stream reaches distributed along Highway 73/175 (black line) in the Laurentides Wildlife Reserve (Québec, Canada). The intensity of shading is proportional to altitude. Dashed lines show the boundaries of four watersheds.

Figure 2. Schematic representation of the 12 stream reaches where redds were recorded in 2007 (thin lines) and 2008 (thick lines). Distances from the highway are provided along the bottom scale for the upstream (negative values) and downstream (positive) sections of each reach. Reaches are identified by milepost distance from south (km 94.59) to north (km 209.08). A section 200 m in length was lost in 2008 for reach 113.32 because of highway construction.

Figure 3. Redd counts and water level during the 2007 and 2008 spawning seasons. Histograms show the number of redds observed each week. The grey lines show the water level recorded at the permanent station installed in reach 143.75. The grey horizontal bars indicate the survey period. *n*: total redd count.

Figure 4. Highway construction impacts on redd counts according to treatment (BB: "before-before"; BD: "before–during"; DA: "during–after"). Symbols refer to before (white circles), during (grey rectangles) and after (black triangles) highway construction. Reaches are identified by milepost distance from south (km 94.59) to north (km 209.08).

Figure 5. Spatial distribution of redds in 2007 (grey) and 2008 (black) shown by kernel density functions. The horizontal grey lines show the stream sections where redds were recorded. Reaches are identified by milepost distance from south (km 94.59) to north (km 209.08). Distances from the highway are positive downstream and negative upstream.

Figure 6. Fine sediments (total mass of sediments < 0.5 mm) sampled by sediment traps from May 2006 to October 2009 in six reaches. Fine sediments were collected before (white circles), during (grey rectangles), and after (black triangles) highway construction. Grey vertical bars represent the 2007 and 2008 spawning seasons. Reaches are identified by milepost distance from south (km 94.59) to north (km 165.93).

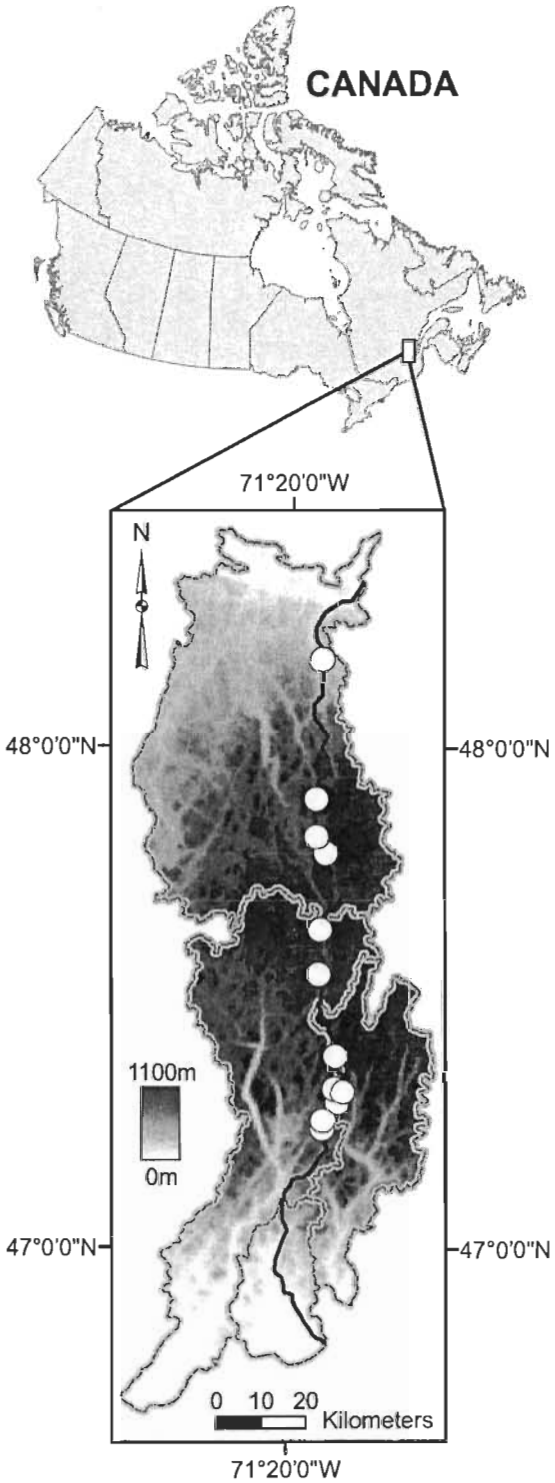
CANADA
71°20'0"W
N
48°0'0"N
48°0'0"N
1100m
0m
47°0'0"N
47°0'0"N
0 10 20
Kilometers
71°20'0"W

Figure 1

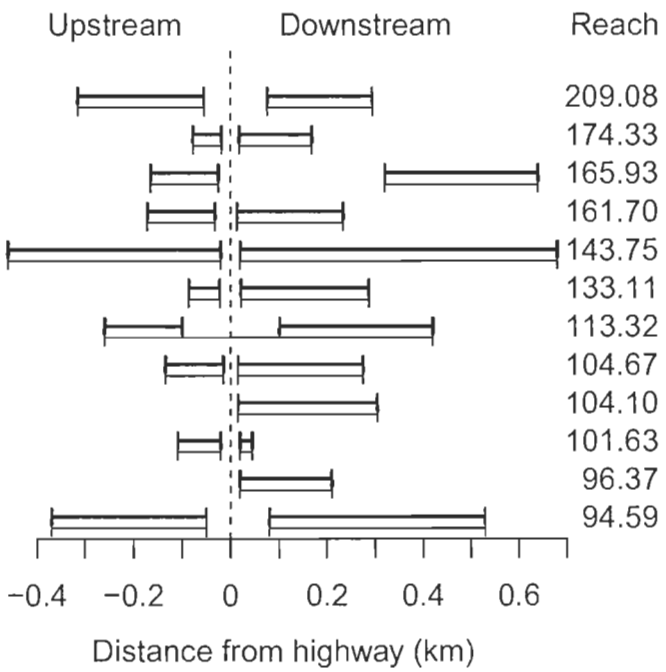
Upstream
Downstream
Reach
209.08
174.33
165.93
161.70
143.75
133.11
113.32
104.67
104.10
101.63
96.37
94.59
−0.4
−0.2
0
0.2
0.4
0.6
Distance from highway (km)

Figure 2

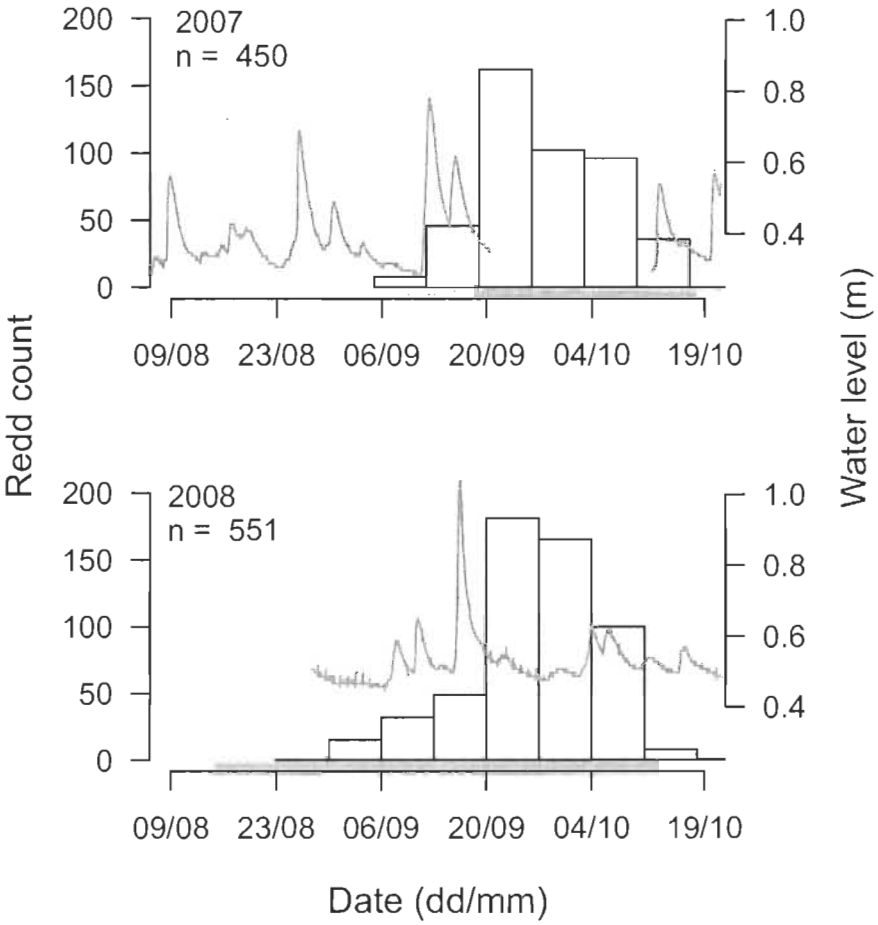
2007
n = 450
2008
n = 551
Redd count
Water level (m)
Date (dd/mm)
09/08
23/08
06/09
20/09
04/10
19/10
0
50
100
150
200
0.4
0.6
0.8
1.0

Figure 3

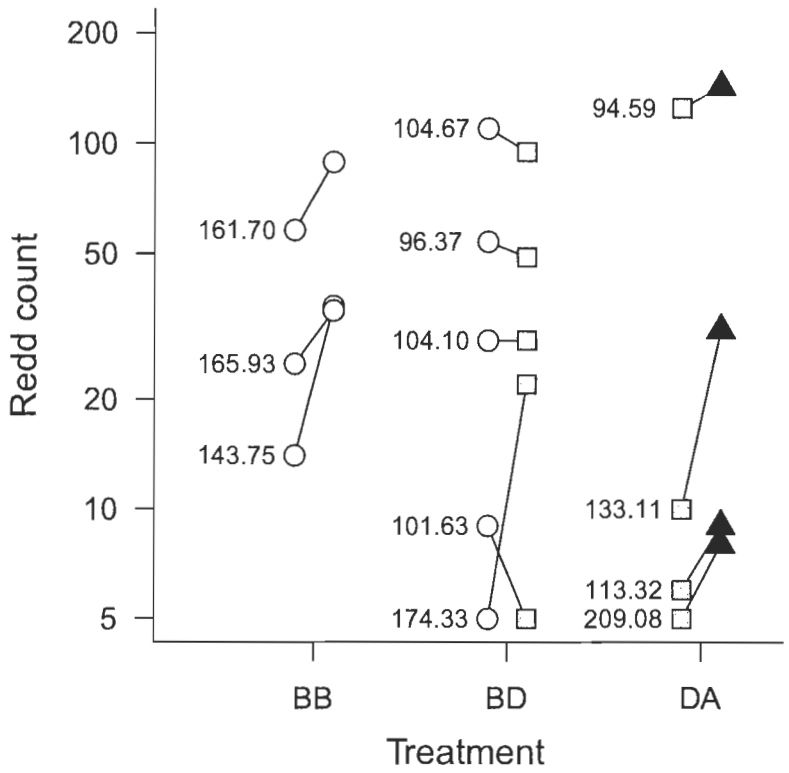
200
100
50
20
10
5
Redd count
161.70
165.93
143.75
104.67
96.37
104.10
101.63
174.33
94.59
133.11
113.32
209.08
BB
BD
DA
Treatment

Figure 4

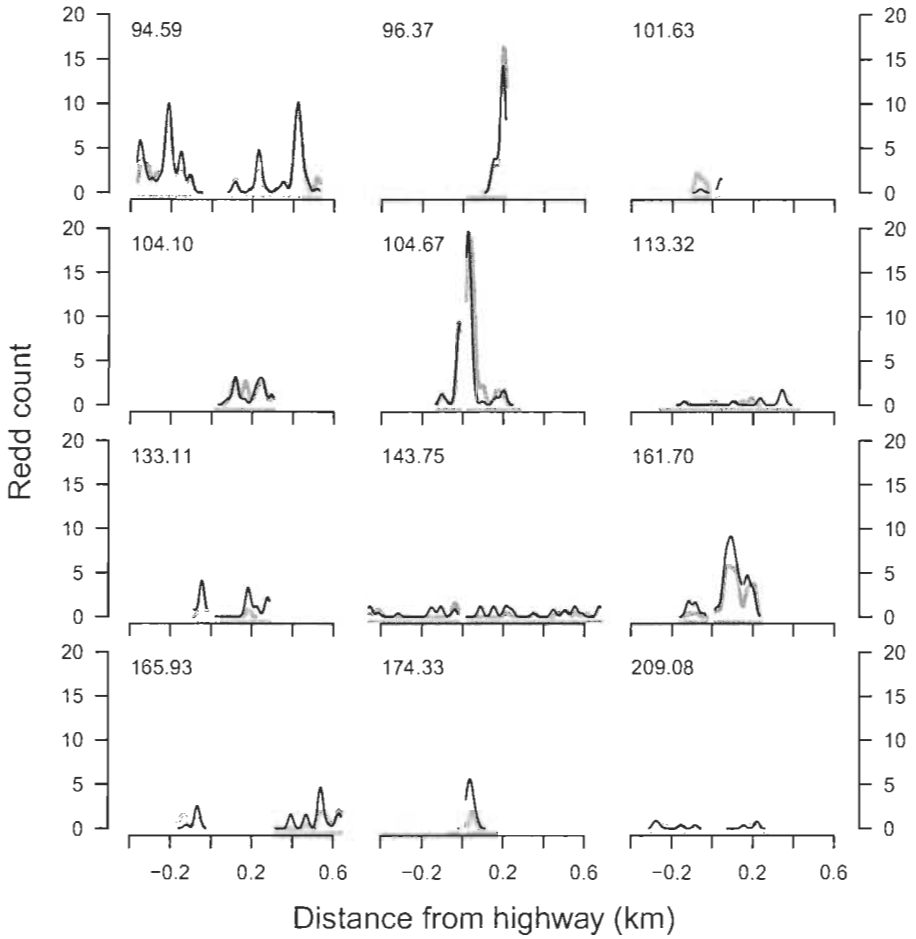
94.59
96.37
101.63
104.10
104.67
113.32
133.11
143.75
161.70
165.93
174.33
209.08
Redd count
Distance from highway (km)
0
5
10
15
20
−0.2
0.2
0.6

Figure 5

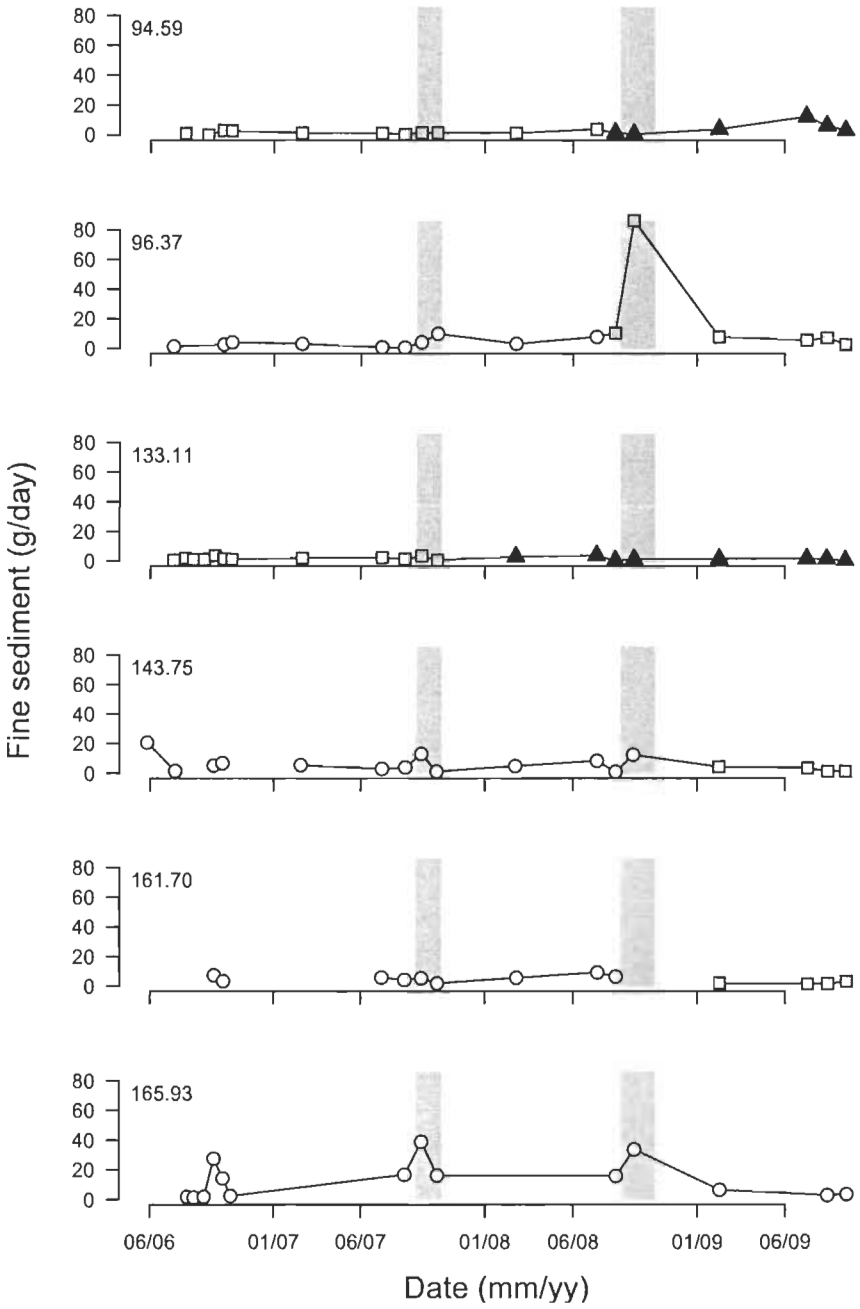
Fine sediment (g/day)
94.59
96.37
133.11
143.75
161.70
165.93
0
20
40
60
80
06/06
01/07
06/07
01/08
06/08
01/09
06/09
Date (mm/yy)

Figure 6

Supporting Information

Video Clip S1. Video clip showing a brook charr female digging into substrate filled by fine sediments. The excavation is clearly identifiable under the female at the beginning of the clip. The female excavated the lower part of the redd three seconds after male courtship (quivering).

DISCUSSION GÉNÉRALE

Synthèse et contributions scientifiques de la thèse

Cette thèse a examiné les impacts de l'axe routier 73/175 sur les populations d'omble de fontaine. Les travaux autoroutiers n'ont causé aucun impact notable sur les densités (chapitre I) et ont engendré une légère diminution du nombre de sites de reproduction (chapitre III). Cette diminution a été ponctuelle et doit être mise en relation avec le contexte environnemental, c'est-à-dire en considérant non seulement les travaux autoroutiers mais aussi les conditions météorologiques dans lesquelles les travaux autoroutiers ont lieu. L'impact majeur de l'axe routier est la fragmentation de l'habitat causée par les traverses dont le niveau de franchissement n'est pas approprié. La restriction des déplacements vers l'amont semble être une explication plausible du surplus des densités observé en aval de ces traverses. Les faibles distances de dispersion en été (chapitre II) suggèrent que cette restriction survient à d'autres étapes du cycle vital. Par ailleurs, les traverses avec substrat naturel ou dotées de déversoirs n'ont pas semblé restreindre les déplacements (chapitre II), ce qui est cohérent avec la distribution spatiale des densités observée pour ce type de traverse (chapitre I). En conclusion, les populations d'omble de fontaine semblent davantage être affectées par les traverses autoroutières que par les activités de construction dans notre système. Cette thèse propose des approches de modélisation pour quantifier l'intensité de la fragmentation causée par ces traverses.

Le chapitre I évalue les impacts autoroutiers sur les densités locales d'omble de fontaine, à l'aide d'un plan d'échantillonnage extensif (Walters et al. 1988, Roedenbeck et al. 2007) et des analyses par modèles mixtes (Wagner et al. 2006). La comparaison de modèles de plus en plus complexes a mis en évidence le rôle prépondérant de la fragmentation de l'habitat causée par les traverses et a dressé un

patron très fin de la distribution spatiale des populations d'omble de fontaine à proximité de l'axe routier 73/175. En particulier, la discontinuité amont – aval des densités constitue une mesure quantitative de la fragmentation de l'habitat qui s'accorde avec notre classification des traverses en fonction de leur niveau de franchissement. La classification utilisée est adaptée aux traverses couramment rencontrées dans le réseau autoroutier et repose sur une simplification de classifications existentes (Love et Taylor 2003, Poplar-Jeffers et al. 2009), dans la mesure où elle ne nécéssite pas d'avoir des données sur le régime hydrologique des cours d'eau. La distribution spatiale des populations d'omble de fontaine répond bien à cette classification simplifiée. De ce fait, alors que les effets de la fragmentation de l'habitat sur les populations de poissons ont été de nombreuses fois documentés pour les barrages (Morita et Yamamoto 2002, Gosset et al. 2006, Meixler et al. 2009) ou des obstacles courts tels les chemins forestiers (Warren et Pardew 1998, Burford et al. 2009, Poplar-Jeffers et al. 2009), une contribution importante du chapitre I est d'avoir quantifié sur le terrain, et à partir d'une variable biologique (la densité), l'effet de la fragmentation de l'habitat causée par les traverses autoroutières sur les populations d'omble de fontaine.

Le cadre de modélisation développé au chapitre II a permi d'estimer à la fois la dispersion estivale des populations d'omble de fontaine et la perméabilité des traverses, à partir de données de marquage – recapture. D'un point de vue fondamental, l'approche proposée, qui étend les modèles conventionnels de dispersion en incorporant l'effet des barrières, devrait aider à la compréhension de la dynamique des populations dans des paysages fragmentés (Lindenmayer et al. 2003, Urban et al. 2009, Lookingbill et al. 2010). En adaptant la fonction de dispersion, il est également possible d'étendre le cadre de modélisation à des déplacements survenant à d'autres étapes du cycle vital (Lucas et Baras 2001, Curry et al. 2002, Buchanan et Skalski 2010). En particulier, les faibles distances de dispersion observées en été au chapitre II suggèrent que l'effet de barrière des traverses identifié

au chapitre I pourrait se manifester au printemps ou à l'automne, périodes auxquelles les déplacements se font sur de plus longues distances (Curry et al. 2002). D'un point de vue appliqué, le paramètre de perméabilité est une mesure fine et instantannée du niveau de franchissement des traverses qui se base sur le comportement des individus (Larinier 2002, Rodríguez 2010) et non sur les caractéristiques physiques des traverses (Ead et al. 2002, Love et Taylor 2003). De plus, l'approche par simulations a démontré qu'il est possible d'appliquer directement notre plan d'échantillonnage sous certaines conditions (par exemple sur des traverses dont la longueur est inférieure à 20 m). De ce fait, le cadre de modélisation développé pourrait facilement être implémenté dans les programmes de suivi environnemental pour l'évaluation de la perméabilité des traverses, à partir de données marquage – recapture récoltées sur le terrain.

Le chapitre III a quantifié les impacts des travaux autoroutiers sur le nombre de sites de reproduction. Les travaux autoroutiers ont entrainé une légère diminution du nombre de sites de reproduction seulement la deuxième année du suivi, ce qui semblait être associé avec la queue de l'ouragan Ike. Si les sédiments pouvaient être retenus efficacement sous des conditions météorologiques normales, l'arrivée d'un événement extrême pourrait favoriser l'érosion et la sédimentation dans les cours d'eau en construction (Douglas et al. 1999). Dans l'ensemble, les faibles modifications du nombre de sites de reproduction et la très grande stabilté de ces derniers, quelque soit le niveau de sédimentation, ont concordé avec l'absence d'effet des travaux autoroutiers sur la distribution spatiale des populations d'omble de fontaine reportée au chapitre I.

Perspectives de recherche

Les échelles spatio-temporelles en écologie : des technologies à la conservation

Le temps et l'espace sont des composantes indissociables de l'écologie. En effet, un système écologique est la résultante de processus agissant à des échelles multiples (Urban et al. 1987, O'Neill et al. 1989, Fausch et al. 2002). Il en résulte que la perception de notre environnement change suivant l'échelle d'observation, qu'elle soit spatiale ou temporelle (Wiens 1989, Levin 1992, Schneider 2001, Dugan et al. 2002, Wheatley et Johnson 2009). La fragmentation et la sédimentation sont des perturbations anthropiques pouvant se manifester à des échelles multiples (Fahrig 2003, Fausch et al. 2010, Molinos et Donohue 2010). Il faut donc réfléchir à la fois au plan d'échantillonnage et aux analyses statistiques à utiliser, surtout pour des questions adressées à grande échelle (Roedenbeck et al. 2007, Fink et al. 2010, Eigenbrod et al. 2011). Cette réflexion a déjà été abordée en introduction générale et au chapitre I. La section suivante, portant sur les simulations, donne des indications supplémentaires sur l'optimisation des plans d'échantillonnage. Les objectifs de cette sous-section sont de faire un survol des limites des trois chapitres en rapport avec les échelles considérées et d'évaluer comment l'utilisation de technologies telles que la génétique, les isotopes stables ou la géomatique aiderait à une compréhension plus globale des impacts des routes sur les écosystèmes. Enfin, l'adéquation entre les échelles écologiques et les politiques de gestion est abordée dans une perspective de conservation (Fausch et al. 2002, Cumming et al. 2006).

La génétique constitue un bon outil pour déterminer la structure spatiale des populations à l'échelle du paysage, avec des applications immédiates à l'écologie des routes (Neville et al. 2006, Holderegger et Wagner 2008, Balkenhol et Waits 2009, Simmons et al. 2010). Au sein d'un réseau hydrographique, l'outil moléculaire a mis en évidence l'isolement des populations suite à la fragmentation de l'habitat (Castric

et al. 2001, Boizard et al. 2009, Griffiths et al. 2009). Le chapitre I a montré comment les densités pouvaient donner une mesure quantitative de la fragmentation de l'habitat, en comparant les densités en amont et en aval des traverses. Par contre, dans des situations où les populations sont capables de se maintenir de part et d'autre de la barrière (Novinger et Rahel 2003, Cook et al. 2010), la génétique offre une mesure de la perméabilié des barrières, en vérifiant si les échanges entre les populations sont possibles. Par exemple, la diminution de la diversité génétique des populations est une mesure de l'effet de barrière aux déplacements (Wofford et al. 2005, Beneteau et al. 2009). Alors que le chapitre II évalue la perméabilité instantanée des barrières, la génétique intègre l'historique des déplacements sur une échelle temporelle beaucoup plus longue (Landguth et al. 2010, Morrissey et Ferguson 2011, Young 2011). Une perspective de recherche prometteuse serait d'intégrer les modèles de dispersion en milieu fragmenté (chapitre II) pour prédire l'évolution génétique des populations (Broquet et Petit 2009, Fayard et al. 2009).

Les isotopes stables sont un complément aux techniques de marquage – recapture pour déterminer l'étendue des déplacements à de grandes échelles spatiales (Cunjak et al. 2005, Rasmussen et al. 2009, Sepulveda et al. 2009). Couplés à des marqueurs génétiques, les isotopes stables de l'azote et du carbone ont mis en évidence l'isolation de populations de perchaude pygmée (*Nannoperca australis*) entre différents cours d'eau d'un même réseau hydrographique (Cook et al. 2007). Le chapitre II a proposé une quantification précise des distances de dispersion, mais le plan d'échantillonnage utilisé a rendu difficile la détection des déplacements sur de longue distance. À l'inverse, les isotopes stables sont une alternative efficace pour caractériser les déplacements à de grandes échelles spatiales, mais la mesure des déplacements est moins précise et la technique exige que les milieux étudiés aient des signatures isotopiques bien distinctes (Jardine et al. 2005, Zeigler et al. 2011). La combinaison des modèles de dispersion développés au chapitre II et des isotopes

stables pourrait être une avenue de recherche intéressante pour étudier la dispersion en milieu fragmenté à l'échelle du paysage.

Les systèmes d'information géographique (SIG) sont très utiles dans l'exploration des relations entre les espèces et leur environnement à plusieurs échelles spatiales (Creque et al. 2005, Wheaton et al. 2010, Firman et al. 2011, Knouft et al. 2011). En particulier, les SIG permettent de vérifier l'influence de l'échelle d'observation sur les conclusions obtenues (Feist et al. 2010, Firman et al. 2011). La stabilité spatio-temporelle des sites de reproduction observée au chapitre III a suggéré que des variables du paysage structurent la disponibilité des zones de reproduction. Les SIG pourraient servir à l'identification de ces variables comme Buffington *et al.* (2004) l'ont fait en caractérisant la disponibilité en substrat de fraie au sein des bassins versants. L'omble de fontaine est une espèce connue pour sélectionner les zones de résurgence (Curry et Noakes 1995, Bernier-Bourgault et Magnan 2002, Guillemette et al. 2011). Ainsi, les variables du paysage caractérisant les résurgences comme les zones de constriction des vallées alluviales confinées pourraient être de bonnes variables prédictives (Baxter et Hauer 2000, Malcolm et al. 2005, White et al. 2010). De façon alternative, la modélisation de l'écoulement souterrain demeure sans doute la meilleure approche pour prédire les zones de résurgence à l'échelle du bassin versant (Kunkel et Wendland 1997, Wiley et al. 1997, Baker et al. 2003). Une application possible serait de vérifier si le déplacement des cours d'eau lors des constructions routières n'entraînerait pas une diminution de l'apport d'eau souterraine et, par conséquent, une diminution de la qualité de l'habitat du poisson (Olsen et al. 2009, Waco et Taylor 2010). Par ailleurs, le chapitre I a mis en évidence la fragmentation de l'habitat engendrée certaines traverses. Toutefois, il reste à quantifier l'habitat réellement disponible en amont de ces traverses afin de pouvoir proposer les traverses à restaurer en priorité (Steel et al. 2004, Meixler et al. 2009, Poplar-Jeffers et al. 2009). La prédiction des zones de reproduction à l'aide des SIG

couplée à la classification des barrières développée au chapitre I serait une avenue de recherche utile à la planification des travaux autoroutiers.

Les politiques de gestion gagnent à être conduites à des échelles multiples (Armstrong et al. 1998, Cumming et al 2006, Peters et al. 2008). L'impact de la sédimentation, par exemple, ne se manifeste pas seulement dans les cours d'eau bordant les routes mais aussi dans les lacs où se déversent ces cours d'eau (Donohue et Molinos 2009). Les traverses, quant à elles, modifient la connectivité du réseau hydrographique, à la fois dans le temps et dans l'espace, et les stratégies de conservation doivent intégrer ces sources de variabilités spatiales et temporelles (Fausch et al. 2002, Ward et al. 2002, Fullerton et al. 2010). Les technologies mentionnées plus haut sont une aide aux plans de conservation : la génétique a permis de définir l'unité spatiale de conservation de l'omble de fontaine en lac (Addison et Wilson 2010) ; les SIG ont mis en évidence que les plans de conservation du saumon chinook (*Oncorhynchus tshawytscha*) seraient plus efficaces s'ils étaient pris à l'échelle du bassin versant (Feist et al. 2003). Dans une perspective de conservation, la gestion des populations d'omble de fontaine suite aux travaux autoroutiers devrait s'inspirer des réflexions faites sur la gestion des populations du saumon Atlantique (*Salmo salar*) qui subit des perturbations similaires mais à des échelles spatiales et temporelles différentes (Armstrong et al. 1998).

Les simulations en écologie : de la théorie à la pratique

L'approche par simulations est une approche efficace, rapide et peu coûteuse en écologie (Peck 2004). Les avancées en informatique et la puissance grandissante des ordinateurs ne sont certainement pas étrangères à la présence de plus en plus grande des simulations dans la littérature scientifique (Baker et al. 1995, Byers 2001, Skarpaas et al. 2005, Okamoto et al. 2009, Rodríguez 2010). Dans cette section, les principaux avantages de l'approche par simulations seront abordés, dont

l'optimisation des plans d'échantillonnage (Benedetti-Cecchi 2001, Skarpaas et al. 2005), le développement de nouvelles méthodes d'analyse (Borcard et Legendre 2002, Tetzlaff et al. 2011), l'aide à la décision dans les plans de conservation (Wennergren et al. 1995, Colchero et al. 2011) et la prédiction de l'évolution des espèces sous des contraintes environnementales et anthropiques (Jaeger et al. 2005, Lawler et al. 2009). La majorité des exemples développés sont en lien avec les thématiques abordées dans la thèse. En particulier, les chapitres I et II illustrent comment les simulations peuvent servir à supporter certaines hypothèses (chapitre I) ou aider à l'interprétation des résultats tout en permettant de développer des pistes de recherche futures (chapitre II). Nous soulignerons à travers ces exemples comment l'approche par simulations constitue une démarche intellectuelle à privilégier lors de la validation et de la mise en pratique de nouvelles théories (Peck 2004, Albert et al. 2010, Rodríguez 2010).

Les simulations peuvent servir d'expérimentations artificielles, utiles à l'élaboration de plans d'échantillonnages adéquats, spécialement lorsque des projets pilotes sont difficilement réalisables (Peck 2004, Meyer et al. 2009). Dans leur synthèse, Zurell *et al.* (2010) soulignent l'importance d'intégrer dans les simulations à la fois les processus gouvernant le fonctionnement des systèmes écologiques (par exemple la dispersion) et la façon dont ces processus sont observés lors de l'échantillonnage (par exemple par marquage et recapture), afin d'obtenir une vision réaliste des phénomènes observés. Les simulations incluant ces deux étapes sont résumées sous le terme unificateur *l'approche écologiste virtuelle* (traduction libre de *Virtual Ecologist approach*). Le principe général, largement partagé dans ce type d'approche, est simple : créer une base de données virtuelles reproduisant le plus fidèlement possible les données susceptibles d'être récoltées sur le terrain et utiliser la même démarche d'analyse que celle utilisée avec les données réelles, afin d'évaluer le meilleur plan d'échantillonnage (Benedetti-Cecchi 2001, Pooler et Smith 2005, Rota et al. 2009, Zurell et al. 2010).

Cette approche par simulations est illustrée ici par des études portant sur la dispersion et sur les perspectives de recherche du chapitre II. Dans les études sur la dispersion des graines, par exemple, cette approche a souvent permis d'évaluer quelle serait la meilleure disposition des trappes afin de bien caractériser les courbes de dispersion (Skarpaas et al. 2005, Pielaat et al. 2006). En rivière, la méthode d'échantillonnage a suscité des débats sur la question des déplacements restreints observés chez les salmonidés (Gowan et al. 1994, Rodríguez 2002). Même si une méthode d'analyse appropriée permet de résoudre une partie du problème (Rodríguez 2002, Fujiwara et al. 2006, Coombs et Rodríguez 2007, Rodríguez 2010), nous avons vu dans le chapitre II que la combinaison des contraintes écologiques (c'est-à-dire la capacité de dispersion) et du plan d'échantillonnage affecte notre facilité à détecter un effet de barrière sur la dispersion. Une approche par simulations pourrait évaluer certaines contraintes du plan d'échantillonnage qui n'ont pas été considérées au chapitre II comme la longueur des sections, la distance d'espacement entre les sections, l'étendue de la zone d'étude, etc. L'optimisation du plan d'échantillonnage permettrait ainsi une quantification plus précise de l'effet de barrière à partir des données de marquage – recapture récoltées sur le terrain.

Un autre avantage important des simulations est de pouvoir valider de nouvelles méthodes d'analyse (Borcard et Legendre 2002, Horton et Letcher 2008). Par exemple, Borcard et Legendre (2002) ont utilisé une série de simulations pour établir les propriétés statistiques et la robustesse d'une méthode d'analyse basée sur les coordonnées principales d'une matrice de voisinage (CPMV) visant à décomposer la structure spatiale des données. L'avantage de connaître très exactement les valeurs des paramètres entrées dans les simulations permet de comparer les paramètres estimés aux paramètres simulés pour juger de la précision et du biais potentiel des méthodes d'analyse (Baker et al. 1995, Samietz et Berger 1997). Tel que mentionné au chapitre II, cette approche permet de s'assurer de la fiabilité des résultats obtenus par la méthode d'analyse sur des données réelles. Évidemment, la fiabilité des

résultats est intimement liée au plan d'échantillonnage, comme cela a déjà été abordé précédemment (Cooper et al. 2008, Rodríguez 2010).

Une vaste application des simulations se retrouve dans la biologie de la conservation. Premièrement, les simulations sont souvent le seul outil disponible pour prédire ce qui pourrait se produire dans le futur, comme la distribution des espèces suite au changement climatique (Lawler et al. 2009) ou, plus proche de notre sujet, l'impact de la fragmentation de l'habitat sur la persistance des populations (Fahrig 2001, Jaeger et al. 2005, Letcher et al. 2007). Deuxièmement, les simulations orientent les plans de conservation, comme le choix de l'emplacement des réserves (Quintana et al. 2010) ou les données à récolter lors des programmes de suivi (Katzner et al. 2007). En lien avec la thèse, il serait intéressant de répondre à deux objectifs dans des recherches futures : (1) développer un modèle prédictif couplant les effets des sédiments (Harvey et Railsback 2009) et de la fragmentation de l'habitat (Letcher et al. 2007) sur la dynamique des populations de l'omble de fontaine, et (2) proposer un programme de suivi à long terme permettant de détecter les changements éventuels au sein des populations. Les simulations du chapitre I supportent l'hypothèse selon laquelle la dispersion pourrait être à l'origine de la distribution des densités observées à proximité de l'axe routier. La stabilité des sites de reproduction reportée au chapitre III, les modèles de dispersion qui sont développés au chapitre II et le plan d'échantillonnage proposé au chapitre I constituent une base solide pour répondre à ces objectifs.

La dynamique des populations au sein d'un réseau fluvio-lacustre fragmenté

Les lacs s'inscrivent dans l'organisation du réseau hydrographique (Jones 2010). Sur le plan structural, ils participent à la qualité physico-chimique de l'eau, apportent des nutriments aux cours d'eau et en régulent le régime hydrologique (Soranno et al. 1999, Martin et Soranno 2006). Sur le plan biologique, les espèces

migratrices comme les salmonidés peuvent transiter entre les habitats lentiques (par exemple les lacs) et lotiques (par exemple les rivières) au cours de leur cycle vital (Josephson et Youngs 1996, Cossette et Rodríguez 2004, Jardine et al. 2005). À l'automne, certains adultes lacustres peuvent migrer dans les cours d'eau pour se reproduire (Josephson et Youngs 1996, Mucha et Mackereth 2008, Heggenes et al. 2009). À l'été, les échanges entre les lacs et les tributaires peuvent aussi survenir chez les plus jeunes, notamment pour des raisons alimentaires ou de refuge thermique (Curry et al. 1997, Cossette et Rodríguez 2004). Devant la complexité de la configuration des habitats et la multiplicité des mouvements, il semble important de s'interroger sur la dynamique des populations au sein d'un réseau fluvio-lacustre. Dans un tel système, nous pouvons porter un nouveau regard sur la thèse et les conséquences de la fragmentation de l'habitat sur les populations d'omble de fontaine. Quelques pistes de recherche sont données dans les paragraphes suivants en lien avec les trois chapitres.

La migration (Dingle et Drake 2007) est une étape du cycle vital de l'omble de fontaine qui n'a pas été abordée dans cette thèse. La fragmentation de l'habitat engendrée par l'homme entrave la migration des salmonidés et représente un des facteurs du déclin des populations (Thorstad et al. 2008, Northcote 2010). Le chapitre I montre une augmentation locale des densités en aval des traverses classées difficilement franchissables et suggère qu'une restriction des mouvements vers l'amont pourrait en être la cause. L'extension des modèles de dispersion du chapitre II aux mouvements de migration (Buchanan et Skalski 2010) permettrait de vérifier si la migration pourrait être à l'origine des patrons observés au chapitre I. Alors que les simulations du chapitre II indiquent que la dispersion sur de courtes distances rendent difficile la détection de l'effet de barrière, l'application des modèles de dispersion aux données de migration, qui, elle, se fait sur de plus longues distances, devrait en améliorer la détection.

Des populations résidentes et migratrices peuvent se trouver mélangées à l'automne lorsque certains adultes lacustres migrent dans les cours d'eau pour se reproduire (Josephson et Youngs 1996, Koizumi et al. 2006, Mucha et Mackereth 2008, Kusnierz et al. 2009). De plus, on reconnaît maintenant la notion de migration partielle, c'est-à-dire es mouvements de migration qui ne concernent qu'une fraction de la population (Kusnierz et al. 2009, Robillard et al. 2011). Les stratégies de résidence ou de migration pourraient avoir des origines génétiques ou être influencées par le contexte environnemental (Mavarez et al. 2009, Curry et al. 2010, O'Neal et Stanford 2011). Les travaux autoroutiers pourraient affecter de façon différente les populations migratrices et résidentes en raison de la spécificité de leur cycle vital. Aussi, la démarche conceptuelle de la thèse pourrait servir de point de départ pour répondre à la question : quelle est la contribution relative des géniteurs de lac et de rivière (chapitre III) dans la réponse des densités à la fragmentation de l'habitat (Chapitre I) et comment les modèles de dispersion (chapitre II) pourraient tenir compte des stratégies résidentes – migratrices dans un milieu fluvio-lacustre fragmenté ?

Lacs et rivières s'inscrivent dans un continuum d'habitats qui peut être fragmenté par les travaux autoroutiers. Les cours d'eau constituent un corridor de dispersion qui structure les populations d'omble de fontaine lacustre sur le bouclier canadien (Bertolo et al. 2008). Inversement, les lacs sont des sources de recolonisation de cours d'eau isolés par des barrières naturelles ou anthropiques (Adams et al. 2001). Il en résulte que le sens de colonisation des habitats (de l'amont vers l'aval, de l'aval vers l'amont, d'un lac à un tributaire, d'un tributaire à un lac...) et l'asymétrie (amont vs. aval) des barrières devraient être plus rigoureusement évalués dans les recherches futures (Cote et al. 2009, Meeuwig et al. 2010). En conclusion, la dynamique des populations d'omble de fontaine gagnerait à être étudiée en intégrant lacs et rivières lors de l'évaluation des perturbations environnementales.

Conclusion

Cette thèse a examiné les impacts d'une autoroute sur les populations d'omble de fontaine en rivière. Le cadre conceptuel de l'écologie des routes en milieu terrestre a été transposé au milieu aquatique en montrant que la restriction des déplacements et la mortalité (par collision pour la faune terrestre et par augmentation de la charge sédimentaire pour les poissons) sont des impacts qui se retrouvent dans les deux milieux. Par ailleurs, l'évaluation environnementale présentée dans cette thèse comprend un plan d'échantillonnage extensif de type BACI et en palier, et des analyses statistiques qui quantifient les impacts tout en tenant compte de la srtucture des données. Le principal résultat de cette thèse est que la distribution spatiale des populations d'omble de fontaine à proximité de l'axe routier est gouvernée essentiellement par le type de traverse et non par les activités de construction. La restriction des déplacements vers l'amont survenant à une autre période que l'été est le mécanisme le plus plausible pour expliquer cette distribution. L'étude des impacts des autoroutes à des échelles spatio-temporelles plus grandes et incluant les lacs au sein du réseau hydrographique est une avenue de recherche intéressante pour dresser un portrait plus complet de la dynamique des populations d'omble de fontaine en milieu fragmenté. Les simulations représentent une approche complémentaire pour comprendre les mécanismes qui gouvernent cette dynamique et pour proposer des plans de gestion en vue de la préservation des populations d'omble de fontaine en milieu fragmenté.

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Le côté rosé des nuages avec ce côté violet
Et de temps en temps du bleu
Le Ciel

Roger Lanfranchi
Les quatre saisons d'Espigoule

Unité

Alors, dans le demi-jour boréal du canyon,
Tout ce qui existe au monde s'estompe,
Et il n'y a plus que mon âme, mes souvenirs,
Et l'espoir de voir un poisson venir à la surface.

Norman Maclean
La rivière du sixième jour